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ANATOMY AND PHYSIOLOGY  
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HUMAN AND COMPARATIVE

CONDUCTED BY

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## THE PALPEBRAL AND OCULOMOTOR APPARATUS IN FISHES: OBSERVATIONS ON MORPHOLOGY AND DEVELOPMENT. By N. BISHOP HARMAN, B.A., M.B. (Cantab.), F.R.C.S. (Eng.), St John's College; *Demonstrator of Anatomy, Cambridge University.*<sup>1</sup> (PLATES I.-VI.)

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THIS research was originally undertaken with the object of examining the motor apparatus of fishes' eyes, with especial

<sup>1</sup> Read at the Meeting of the Anatomical Society of Great Britain and Ireland, July 1899, and at the British Association, Dover, 1899.

The first of these is the *Chondrostei*, which is a group of fish that are characterized by their cartilaginous skeletons. They are found in both freshwater and saltwater environments. The second group is the *Acipenseridae*, which includes sturgeons and paddlefishes. These fish are also characterized by their cartilaginous skeletons and are found in both freshwater and saltwater environments. The third group is the *Polypteridae*, which includes the bichir. This fish is found in freshwater environments and is characterized by its bony plates and long, pointed snout.

The fourth group is the *Chimaeridae*, which includes chimaeroids. These fish are found in saltwater environments and are characterized by their cartilaginous skeletons and unique body shapes. The fifth group is the *Rajidae*, which includes rays. These fish are found in both saltwater and freshwater environments and are characterized by their flattened bodies and cartilaginous skeletons.

The sixth group is the *Squalidae*, which includes sharks. These fish are found in both saltwater and freshwater environments and are characterized by their cartilaginous skeletons and various body shapes. The seventh group is the *Scyliorhinidae*, which includes dogfishes. These fish are found in saltwater environments and are characterized by their cartilaginous skeletons and various body shapes.

## PARAPHYTES

### Chondrostei:

#### *Acipenseridae*

##### *Chondrosteus*

##### *Chondrosteus*

*Chondrosteus nasus* (Blue Shark).

*Zyzzia nasus* (Hammerhead).

*Chondrosteus vulgaris* (Sticker Dog-fish, Sweet William).

*Chondrosteus lavis* (Smooth Hound).

##### *Scyliorhinidae*

*Scyliorhinus canicula* (Larger spotted Dog-fish).

*S. catulus* (Lesser spotted Dog-fish).

##### *Spinacidae*

*Acanthias vulgaris* (Spiny Dog-fish).

##### *Rhinidae*

*Rhina squatina* (Angel- or Monk-fish).

##### *Batoidei*

##### *Torpedinidae*

*Torpedo narce* (Torpedo Ray).

##### *Rajidae*

*Raja batis* (Common Skate).

*Raja blanda* (Blond Ray).

##### *Holocephala*

##### *Chimaeridae*

*Chimaera monstrosa*.

*Callorhynchus antarcticus*.<sup>1</sup>

### Chondrostei:

#### *Chondrostei*

##### *Acipenseridae*

*A. sturio* (Common Sturgeon).

##### *Polypteroidi*

##### *Polypteridae*

*Polypterus bichir*.<sup>1</sup>

<sup>1</sup> Not dissected.

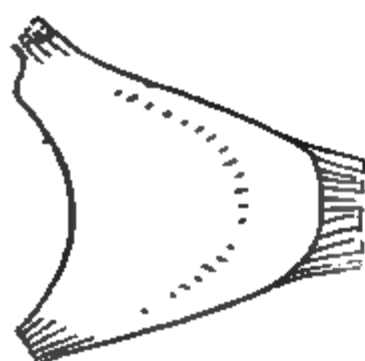


Fig. 1.

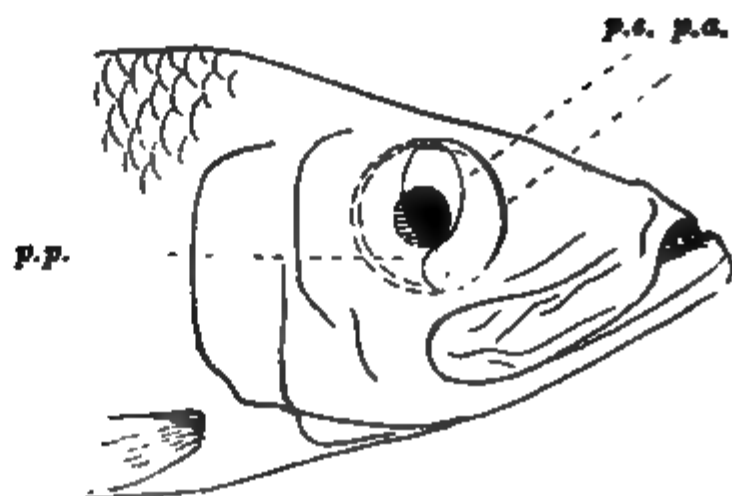


Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.



Fig. 6.



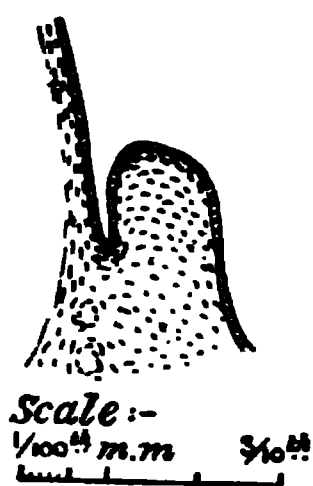


Fig. 7a.

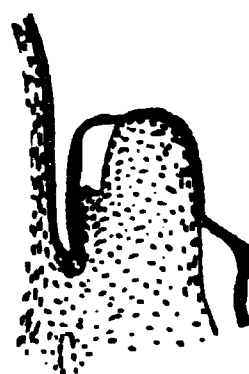


Fig. 7b.

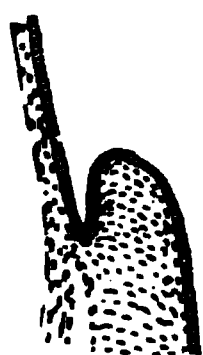


Fig. 8a.

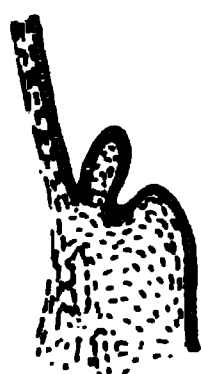


Fig. 8b.



Fig. 8c.

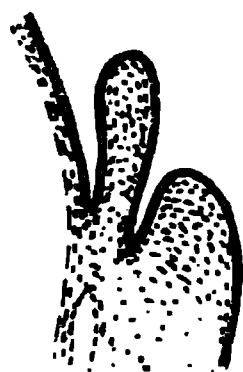


Fig. 9a.

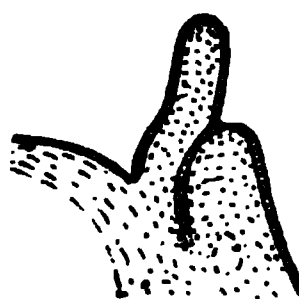


Fig. 9b.

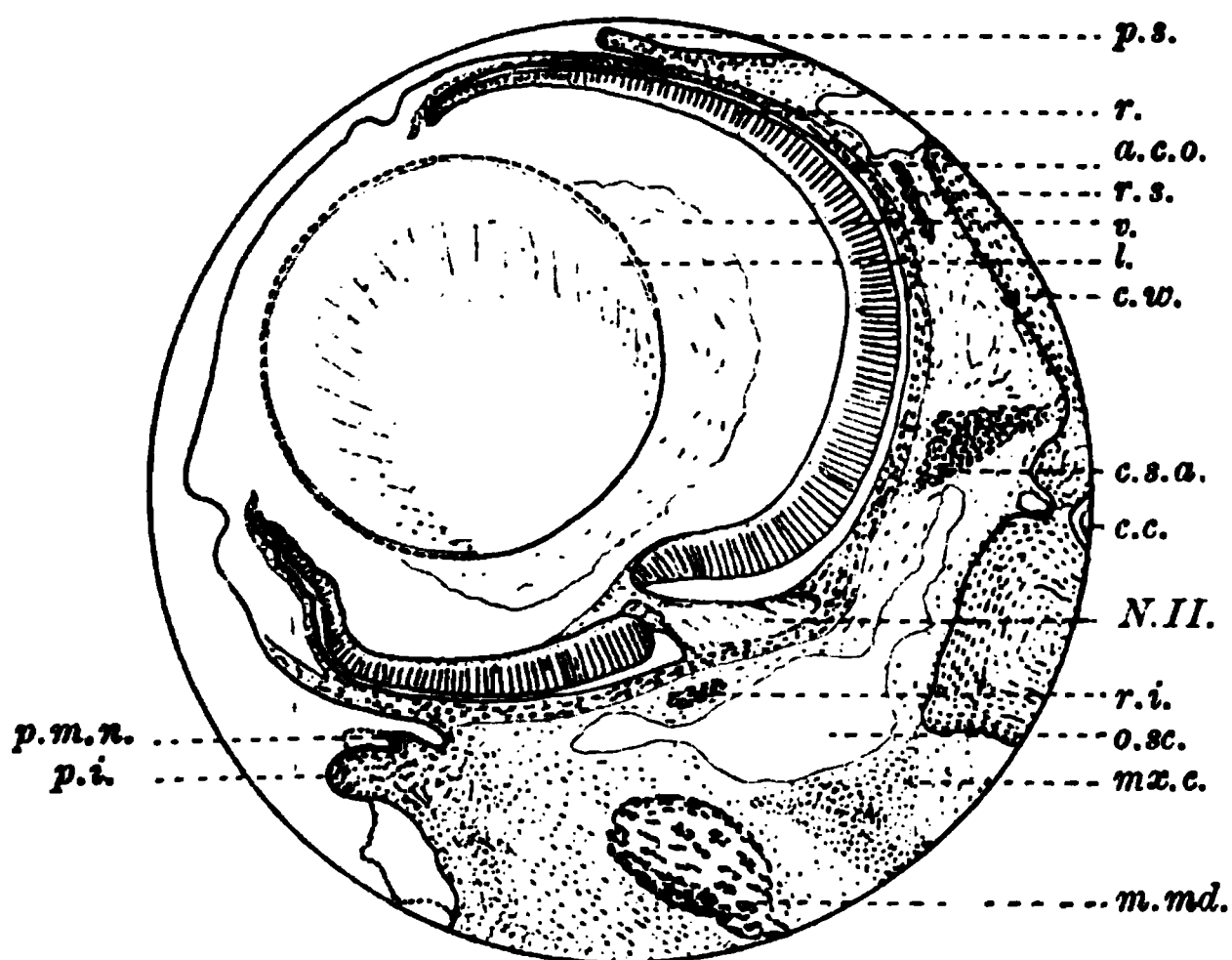


Fig. 7c.





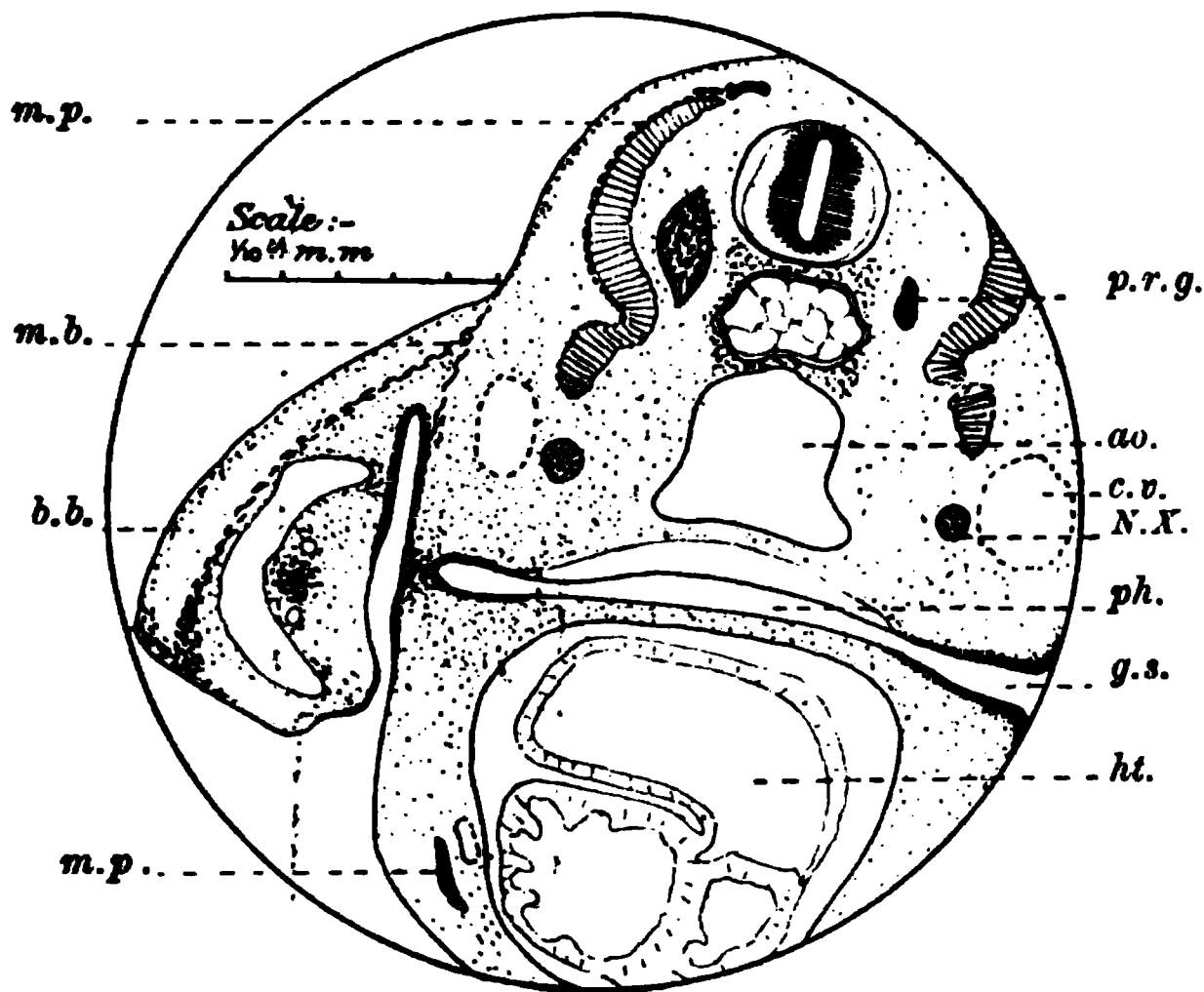


Fig. 10.

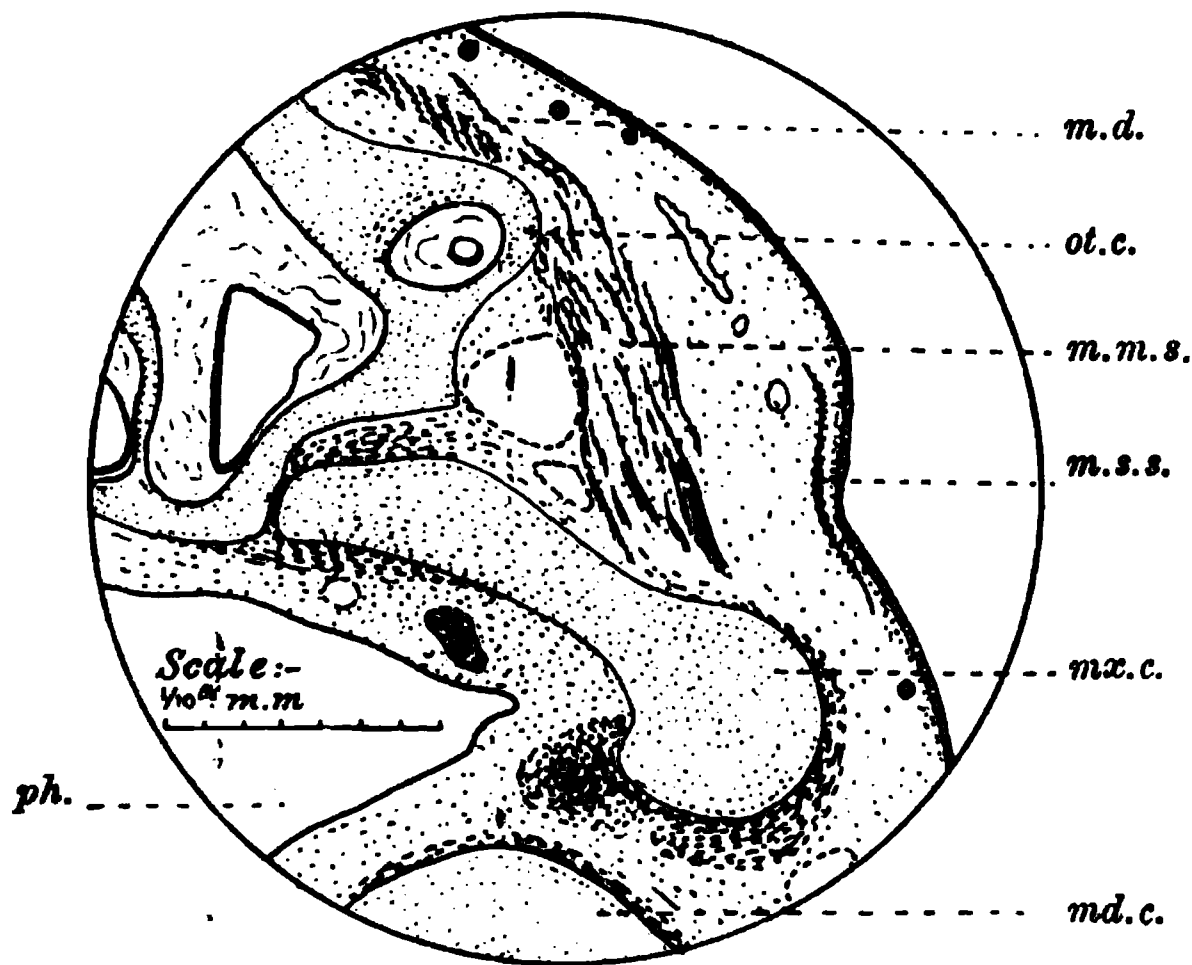


Fig. 11.



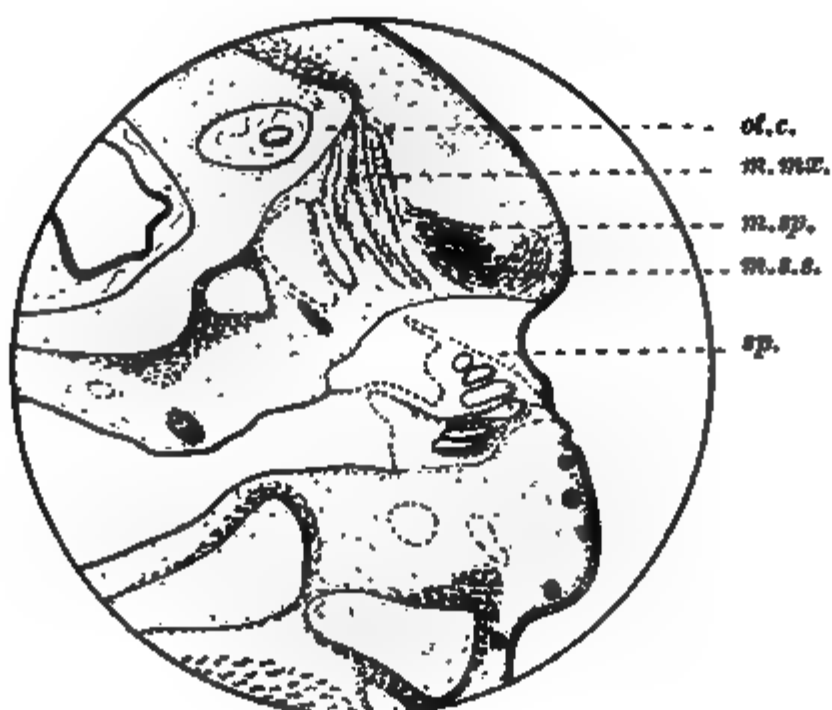


Fig. 12.

p.

id.

Fig. 13.

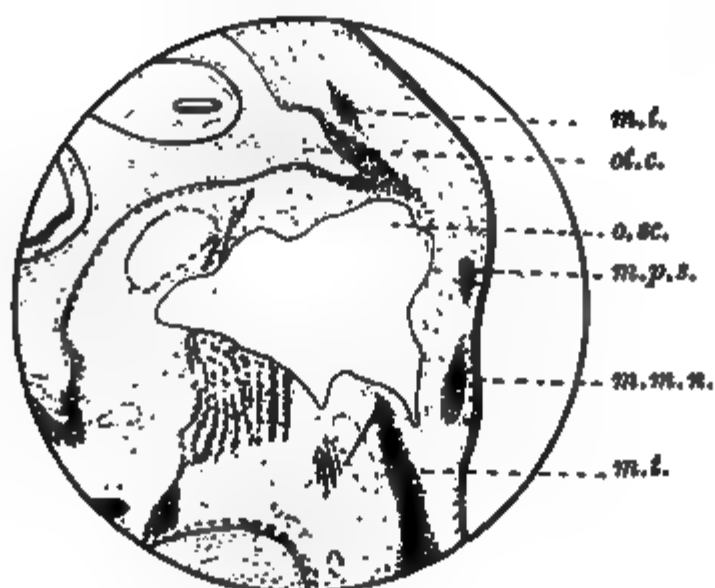


Fig. 14.



|          |          |
|----------|----------|
| r. a. -  |          |
| r. s. -  |          |
| r. il. - |          |
| ol. c. - |          |
| c. s. -  |          |
| p. -     |          |
| sp. -    |          |
|          | . a. i.  |
|          | - r. v.  |
|          | - N. II. |
|          | . o. s.  |
|          | - p.     |
|          | - N. n.  |
|          | - f.     |
|          | - N. v.  |
|          | . o. i.  |

Fig. 15.

|             |         |
|-------------|---------|
|             | c. w.   |
| o. sc. r. - |         |
| p. f. -     |         |
|             | - c. c. |
| p. s. -     |         |
|             | - f. o. |
| p. m. n. -  |         |
| p. i. -     |         |
| o. sc. r. - | - N. v. |
|             | .. ph.  |
|             | - md.   |

Fig. 16.

- r. a.  
 - r. s.  
 - N. II.  
 - o. w.  
 - l. i.  
 - r. il.  
 N. IV.  
 o. i.  
 o. s.

Fig. 17.





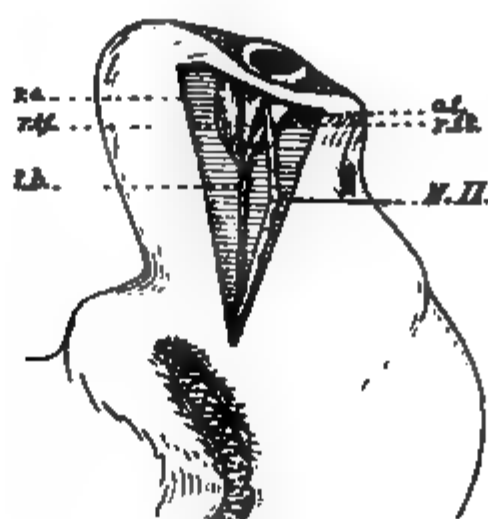


Fig. 18.

- r.s.  
- N.II.  
- r.ii.  
r.s.  
o.s.

Fig. 19.

N.III.  
r.s.  
r.s.  
r.ii.  
N.IV.  
N.II.  
- o.s.  
- o.i.  
  
- o.s.2.

Fig. 20.



TELEOSTEI.

**ACANTHOPTERYGII.**

*A. perciformes.*

Percidæ.

*Perca fluviatilis* (Freshwater Perch).

*Labrax lupus* (Bass).

*Lucioperca sandra* (Pike-perch, Zander of Rhine).

Mullidæ.

*Mullus barbatus* (Red Mullet).

Sparidæ.

*Cantharus lineatus* (Old Wife, Black Sea-bream).

*Pagellus centrodontus* (Common Sea-bream).

*A. cotto-scombriformes.*

Carangidæ.

*Caranx trachurus* (British Horse Mackerel).

Cyttidæ.

*Zeus faber* (John Dory).

Scombridæ.

*Scomber scomber* (Mackerel).

*Thynnus thunnina* (Tunny-fish).

Pediculati.

*Lophius piscatorius* (Angler, Sea-devil).

Cottidæ.

*Trigla pini* (Red Gurnard).

*A. gobiiformes.*

Gobiidæ.

*Periophthalmus Koelreuteri*.

*Callionymus lyra* (Dragonet).

*A. mugiliformes.*

Mugilidæ.

*Mugil chelo* (Grey Mullet).

*A. gastrosteiformes.*

Gastrosteidæ.

*Gastrosteus aculeatus* (Stickleback).

**ANACANTHINI.**

*A. gadoidei.*

*Gadus morrhua* (Cod).

*G. æglefinus* (Haddock).

*G. merlangus* (Whiting).

*G. luscus* (Pouter Whiting).

*Merluccius vulgaris* (Hake).

*Molva vulgaris* (Ling).

Ophidiidæ.

*Ammodytina tobianus* (Sand Eel).

Macruridæ.

*Macrurus coelorhynchus*.

*A. pleuronectoidei.*

Pleuronectidæ.

*Hippoglossus vulgaris* (Halibut).

ANACANTHINI—*contd.**A. pleuronectoidei.*

## Pleuronectidæ.

Hippoglossoides platessoides (Rough Dab).

Rhombus maximus (Turbot).

R. lævis (Brill).

Arnoglossus laterna (Scaldfish)

Pleuronectes platessa (Plaice).

P. flesus (Flounder).

Solea vulgaris (Sole).

S. aurantiaca (Lemon-sole).

Platessa cynoglossa (Pole or Witch).

## PHYSOSTOMI.

## Cyprinidæ.

C. carpio (Carp).

Leuciscus rutilus (Roach).

L. erythrophthalmus (Rudd).

Tinca tinca (Tench).

Abramis brama (Common Bream).

A. blica (White Bream).

## Scombresocidæ.

Belone (Gar-pike).

## Esocidæ.

Esox lucius (Pike).

## Salmonidæ.

Salmo salar (Common Salmon).

S. ferox (Lake-trout).

Osmerus eperlanus (Smelt).

Argentina silus.

## Clupeidæ.

Clupea harengus (Common Herring).

C. sprattus (Sprat).

C. alosa (Shad, Mai-fisch of Rhine).

## Murænidæ.

Anguilla anguilla (Freshwater Eel).

Conger conger (Sea Conger).

## LOPHOBRANCHII.

## Syngnathidæ.

Nerophis lumbriciformis (Little Pipe-fish).

## PLECTOGNATHI.

## Gymnodontes.

Tetrodon lagocephalus (Globe-fish).

Orthogoriscus mola (Sun-fish).

## CYCLOSTOMATA.

## Petromyzontidæ.

P. fluviatilis (Lamprey).

## I. PALPEBRAL APPARATUS.

Within the range of fishes included in the above list there can be found every form of provision for the setting and protection of the outer surface of the bulb, from the most simple and least developed to a complex and highly developed mechanism. Such a series might naturally be expected to be concurrent with an evolution from the simpler to the more complex type of fish, but such a parallelism in development cannot be held to be a real one, since in most cases the complex forms of palpebræ are found in fishes classed within orders nearest the main line of phylogeny, whilst the simpler forms may be found in the more specialised types. This would appear to indicate that the variation of these accessory organs depends peculiarly upon the conditions of life of any particular family, which suggestion is confirmed by the variations of form found in closely allied species.

1. *Palpebral Provision—None.*

There are some, but not many, species in which these negative conditions are found. The actual arrangement of the transition from the skin surrounding the orbit to the outer corneal layer is of two kinds. One in which the passage is by an uninterrupted and even layer of skin which is directly continuous with the transparent outer corneal layer. This arrangement necessarily restricts the movements of the eyeball within the narrowest limits. It is found well exemplified in the common and Conger Eels, also the Lamprey and Globe-fish; in the Conger its influence upon the bulbar muscles is marked. It is also found in a less degree in the commoner Rays.

A second form is that in which the skin passes from the orbital margin to the outer corneal layer by a loose and flexible collar of skin, which allows of free bulbar motion in all the combinations of rotation and rectilinear motions, and also in some cases of projection and retraction. This arrangement can best be seen in the Pleuronectes, where the projection of the bulb allowed by this arrangement gives the eyes of these fishes an appearance not unlike a miniature conning-tower. A similar condition less well marked is found in the Angler.

## 2. *Palpebral Margins and Conjunctival Fornices defined.*

This form is the one found in the majority of the teleostean fishes. The skin passes from the circular orbital margin towards the centre of the cornea, and after extending thereto in a greater or lesser degree, recurves deeply, forming a palpebral margin. The depression formed by the continuance of the thin inner or conjunctival layer on to the bulb to blend with the outer corneal layer, constitutes the conjunctival fornix. This arrangement, other things being equal, allows of great freedom of rotation and rectilinear movements, according to the depth of the conjunctival fornices. The depth to which the folds extend may differ in the lower and upper parts, but since the angles of the eye are rarely defined, the passage from superior to inferior fornices is uninterrupted.

The circular palpebral margin is in life upon a level with, or makes a gentle slope towards, the flat corneal surface, so providing for the least resistance to water friction during progression.

Such palpebral margins, however, afford but little protection to the eye since the greater part of the cornea remains exposed, but in some species, *e.g.* Sturgeon, the margin is sufficiently wide and of dense tissue, with calcified epidermis, that it makes an efficient protection to the sclero-corneal junction.

Of the condition in which the margin and fornices are small and shallow, the Torpedo (inferior fornix only), Chimæra, Perch and Perch-pike, Gurnard, Grey Mullet, Stickleback, Cod, Haddock, Hake, Carp, Roach and Rudd, and the little Pipe-fish, may be taken as examples; and for the broader margins and deeper form of fornices the Sharks, Sturgeon, Bass, Red Mullet, Bream (sea and fresh), Mackerels, Tunny-fish, Whiting, Ling, Tench, Pike, Salmon, and the Herring. These examples do not allow of any classification into families or according to the habitat of the fish as do other structural variations, for differences are found between closely allied members of the same family, *e.g.* amongst the Cods. Thus in Cod, Haddock, and Hake the margins are narrow and the fornices shallow, whilst in Whiting and Ling the margins are fairly broad and the fornices deep.

### 3. *Extra Palpebral Folds*—" *Pseudo-Membranæ Nictitantes*." (Figs. 1 and 2.)

In the salmon the palpebral margin is of irregular shape. In a condition of repose the larger and posterior part of the margin coincides with the corresponding two-thirds of the corneal margin. From here the upper and lower margins continue anteriorly in gradually converging lines to meet in a curve representing a segment of a smaller circle than that of the corneal margin. The space between this anterior margin and the anterior corneal margin, representing a breadth of about one-third the corneal diameter, is filled by a triangular block of muco-areolar tissue<sup>1</sup> of semi-cartilaginous consistency (fig. 1). Its thin posterior edge is transparent and coincident with the corneal margin, except at its upper horn, where it recedes to its upper attachment. The anterior and thicker part is less transparent, and contains a few scattered pigment spots. The triangular block is attached to the anterior palpebral fold by the edges of its superficial surface by means of a thin conjunctival membrane which produces a conjunctival recess; a like attachment from its deep surface to the bulb produces a second and deeper conjunctival recess.

The angles of the cartilaginous block are affixed to the neighbouring bones by three ligaments, the anterior and strongest ligament to the lacrymal bone, the superior to the supraethmoid, and the inferior to one of the suborbital ossicles; the anterior edges of the block overhang a pair of diverticula of the nasal pouch. Dissection of this extra fold in *Argentina silus* and the Trout shows a similar construction.

In the common Herring there exists an extra fold similar to that of the Salmon tribe, but more complete in its formation (fig. 2). In this fish the corneal surface is exposed only in a narrow vertical palpebral fissure formed by the help of three folds, two anterior and one posterior. Of the anterior and posterior each forms a broad thin transparent fold, which is directly and smoothly continuous from the surrounding skin to its thin free edge, where, recurving sharply, it makes a deep conjunctival fornix, and within the anterior fold the extra fold

<sup>1</sup> This constitution was shown by microscopic examination.

is found. At the dorsal extremity of the palpebral fissure is a union of all three folds, anterior, 'extra,' and posterior; the ventral extremity, however, is not so formed, for the posterior fold makes a sharp curve convex anteriorly, which is overlapped by a similar convexity existing on the lower horn of the 'extra' fold. The separation of anterior and 'extra' folds extends for fully two-thirds of the extent of the latter, and results in the formation of a well defined extra conjunctival recess. The two folds blend for their lower third.

The measurements of the depths of the fornices in a medium-sized fish were:—

|  |        |
|--|--------|
| Posterior fornix, . . . . .            | 10 mm. |
| Superficial anterior fornix, . . . . . | 5 mm.  |
| Deep anterior fornix, . . . . .        | 4 mm.  |

The same blind diverticula from the nasal pouch exist beneath the anterior edges of the extra fold of the Herring, as in the Salmon.

The Maifisch presents a modification of this structure owing to the greater fusion of the two anterior folds, so that the sulcus separating them is small, and occupies a position in the anterior-superior region of the eye. There is also a rather narrower palpebral fissure than in the common Herring.

In the common Mackerel there is a narrow vertical palpebral fissure, but the anterior folds are here completely united, a shallow groove only indicating a double arrangement, as in the Herring, whilst in the Horse Mackerel the whole anterior margin is so reduced as to be almost unrecognisable.

This extra fold or false nictitating membrane has been noted in the Salmon by Rosenthal (26, p. 398), who says "there is heaped up at the anterior angle of the eye an immobile gelatinous mass, which forms so as to say a rudimentary 'Nickhaut,' and which fills a part where the bony wall of the orbit is incomplete"; and in a later paper (27, p. 419) he makes a similar suggestion as to the use of the fold. John Hunter (16, p. 413) appears to have noted its presence, but his description is not so certain.

The structure is shown in almost all the species of Salmonidæ delineated in the beautiful plates of Agassiz and Vogt (2),



and its position is indicated by Günther (11) in several outline drawings of Salmons' heads. No mention of it is found in Haller's work on these fish (12).

The structure may probably be considered as filling the gap in the orbital wall as suggested by Rosenthal. It will also serve to protect the eye from injury by its acting as a 'fender.' The large extensions of the margins of both 'extra' and posterior folds in Herrings tends to support this view. Whilst in the absence of any means of regulating the relations of the folds to the pupil, the tissue forming them retains a considerable delicacy and transparency of substance at the edges. It is noteworthy that this structure is developed in fishes frequenting shallow waters and rivers, where such a protection would be especially advantageous.

#### 4. *The Nictitating Membranes of Selachians.*

My dissections of British fish possessing this membrane were completed at Plymouth in Easter 1898, after which date I commenced to work at its development. In June of that year Dr Ridewood (25) read before the Anatomical Society a paper dealing with the same subject from his observations on dissections of adult fish. As this paper has covered the ground for the adult morphology, and the descriptions of the myology are excellent in their accuracy and lucidity, I can add nothing to the anatomy of the musculature.

Regarding Ridewood's suggestion of the possibility of the existence of a nictitating apparatus in the horizontal duplicature of skin below the eye of Scyllium, Wiedersheim shares this view, for he has included *S. canicula* with other fish already recognised as possessing the membrane (35, p. 431). Regarding the movements of the eyelids of this fish, it may be pertinent to record my observations. I had had doubts as to the free mobility of the lids by the muscles attached thereto, by reason of the toughness of its skin, but these doubts were dissipated by some observations made on the fish within one of the tanks of the Brighton Aquarium. I saw a specimen of the Larger Spotted Dog-fish slowly gliding towards me, and when within a few inches of the glass front of the tank, and of my eyes, the

creature gave a most unmistakable wink, by which the whole eye seemed to be covered by the lids. The succeeding day I was able to make a longer observation on a specimen of the Smaller Spotted Dog-fish ; the fish was lying motionless on the gravelled floor of the tank and in contact with the glass front ; a crab approached and walked over the dog-fish's head ; the only sign of a sensitiveness on the part of the fish to this act of aggression was the complete closure of its eye.

In this action the greatest part was played by the nictitating membrane, *i.e.*, the upper of the two folds constituting the whole lower eyelid (fig. 6). Assistance came from the straightening, depression, and slight eversion of the upper lid so as to completely fit over the nictitating membrane. The elevation of the membrane was so complete that the deep sulcus normally existing between the membrane and the lower lid was almost obliterated, and the lower lid was itself slightly elevated with the extension of the nictitating membrane.

Regarding the relative values of the eyelids of *Carcharias*, *Zygæna*, *Galeus*, *Mustelus*, and *Scyllium*, it appears, from an examination of the palpebral apparatus of all vertebrates, that the trend of progression in the evolution of these structures is towards a greater completeness in the organisation of the upper and lower lids, and that the condition of the nictitating membrane is one of secondary importance. With this proposition in view, a comparison of the apparatus in *Carcharias*, *Zygæna*, and *Galeus*, with that found in *Mustelus* and *Scyllium* (figs. 3, 4, 5, and 6), will show that although the former group presents a marked specialisation of the nictitating membrane, yet its true upper and lower lids are feebly developed, since they inclose a large round palpebral fissure which would leave the eye exposed and unprotected were it not for the development of this highly specialised secondary membrane. On the other hand, in *Mustelus* and *Scyllium* the palpebral fissure is oval and the bulb receives a considerable screen from upper and lower lids as well as from the membrane, and both the true lids can be moved in the defence of the eye, so that the excursion required of the membrane not being so great, its specialisation is arrested. It will therefore follow that in these latter fish, *Mustelus* and *Scyllium*, we have a nearer coincidence with the line of progres-

sive evolution than in *Galeus*, *Carcharias*, and *Zygæna*. To substantiate this proposition it is necessary to show that the development of the membrana nictitans (*i.e.*, the inner fold of the lower lid) is later in date and secondary in site of origin to the true lower lid.

#### 5A. *The Development of the Membrane—Previous History.*

The earliest suggestion regarding its origin appears to be that given by Müller (23, p. 121): he states that it is a duplicature of the skin growing from the inner surface of the eyelid. On what ground this statement is made I cannot discover, for he does not add any reasons for the opinion given. I can only believe that it is made from an analogy of the position of the membrane in the shark and that in the bird, for in his description of the naked-eye appearance of the fish's membrane, he contrasts it with the delicate conjunctival structure of the bird. Subsequently Müller's statement has been repeated in the text-books of Balfour (3, p. 416), Wiedersheim (35, p. 434), Hertwig (13, p. 431), and others; whilst Minot (22, p. 727) states that "nothing accurate is known concerning its development."

I am unable to find any further hypothesis as to its origin, or attempted elucidation of its development, until we come to that contained in the paper by Ridewood. This zoologist follows an exceedingly interesting and suggestive line of argument based upon the variations in the form of the membrane in the adult fishes possessing it. He notes the fact that the membranes of *Galeus* and *Mustelus* differ in their 'finish': the opposing surfaces of the lower lid and membrane in *Galeus* and *Carcharias* are free from shagreen, whilst in *Mustelus* the inner surface of the lower lid possesses shagreen. From this he argues that the nictitating membrane is the old lower lid, whilst the present lower lid is a new duplicature of skin, which by the specialisation of the lids in *Galeus* has lost its shagreen, but the structures in *Mustelus* being incompletely evolved have not yet thrown off this internal armature of denticles.

This line of argument, apart from my observations on embryos, I believe to be open to criticism, for it is equally

permissible to apply the facts adduced in support of a conclusion the direct reverse of the one just quoted, namely, that since in the *Galeus*, etc., the proper lids are deficient in growth, the deficiency is made good by an extra mobility of the membrane, and consequently the contiguous epiblast of the lower lid remains free from shagreen; whereas, on the other hand, the reason why in *Mustelus* shagreen is developed to a slight extent upon the contiguous surfaces of lid and membrane is that the membrane of these fishes has ceased its evolution or is on the downgrade, the more extended growth of the true lower lid being followed by a limitation of growth of the membrane, and an extension of calcification of surface epiblast. It is the development of the lids, I would repeat, and not of the nictitating membrane, which is a mark of progressive evolution. This argument I believe to be the true one. It will accord with the variations in the musculature,—the differentiation of form and scope of function is wider in *Galeus* than *Mustelus* or *Scyllium*,—and finally it is supported by actual observations of the origin of the membrane in embryos.

With regard to *Acanthias*, I am still in doubt as to the mobility of its palpebral folds; muscles are found in connection with them; they are figured by Vetter (34, pl. xiv. fig. 3) and Ruge (28, fig. 14); but although I watched the movements of captive specimens of this fish for long times, I did not succeed in observing any movement of the lids.

#### 5B. *The Development of the Membrane—Observations on Embryos.*

The development of these structures I have followed in *Mustelus* embryos obtained from the Naples Marine Station. Four specimens have been used of the lengths of 18, 30, 38, and 48 mm. Of these, the first, second, and third correspond fairly well to the stages 'N,' 'P,' and 'Q' of Balfour (4, p. 79); the fourth has advanced beyond the last of this series, but might correspond to a stage 'R' were this series continued. I shall accordingly refer to them under these letters.

| Length of Embryo. |     | Stage and Letter. |                   |
|-------------------|-----|-------------------|-------------------|
| 18 mm.            | . . | 'N,'              | Balfour's series. |
| 30 mm.            | . . | 'P,'              | do.               |
| 38 mm.            | . . | 'Q,'              | do.               |
| 48 mm.            | . . | 'R,'              | do. continued.    |

In the first of these, 'N,' the bulb has arrived at that degree of development where the cavity of the lens is almost filled with the exuberant growth of its posterior cells, but is still apparent as a narrow sharply-curved slit in the transverse section. Also, the cavity of the optic cup exists at its extremities, whilst at the posterior pole the two layers are nearly in contact. The channel of the optic stalk is pervious, so that the cerebral vesicles are in connection with the cavity of the optic cup. No cartilage has appeared in the mesoblastic cranial covering, but occasional patches of denser tissue indicate the sites of growth of the walls. The ocular muscles are already developed, but there is no indication of the formation of a definite optic capsule.

In embryo 'P' the development has advanced considerably. The lens cavity is wellnigh closed, that of the optic cup is only distinguishable at its extreme edge and in the immediate neighbourhood of the entrance of the optic nerve. This structure is now recognisable as a nerve, and the cavity of the original stalk has disappeared. The cranium presents a growth of cartilage in its floor, which is extending up the side walls to the lateral edges of the roof. An investment of closely-packed cells around the retina shows the formation of an optic capsule.

Embryo 'Q' is an advance upon the former in size, and in the increase of the complexity of its parts and the greater completeness of its cartilaginous skeleton. The optic capsules are well defined, but are not yet cartilaginous.

In embryo 'R,' a delicate layer of cartilage has appeared within the optic capsule, the retina shows stratification, and the cranial skeleton is well grown.

In the earliest of these embryos, 'N,' there is no sign of palpebral growth, the bulb is invested on its external aspect by a uniformly smooth covering of surface epiblast which takes a bold curve, convex outward, due to the supporting optic cup and lens. A considerable interval exists between this epiblastic covering and the sunken epiblast of the lens, for as yet no mesoblast has penetrated the space. The angle made by the passage of the ocular investing epiblast to the general investing epiblast is acute, and in the dorsal region it amounts to a fairly deep recess, but the overhanging bulge does not represent the

commencing palpebral folds, which are seen in the succeeding embryo to grow from the bulbar investment.

In embryo 'P' (figs. 7 *a*, *b* *c*) the sections in the anterior region of the eye show the growth of the upper and lower lids as rounded protuberances arising from the bulbar investment, the upper some distance from, and the lower much nearer the side of the head; of the two, the lower fold is the stouter. In sections more posterior, the earliest growth of the membrana nictitans can be distinguished as a small tongue of dermal tissue appearing upon the ocular side of the lower lid. In the anterior sections it is sessile, but it becomes more tongue-shaped towards the posterior region. In this embryo the epidermis is unfortunately loosened from portions of the environing dermis of both eyes, but this does not at all invalidate the evidence of the specimen, as the dermis is the determining factor of the growth of these structures, and in all the sections the definition of the cells of both layers is quite clear—they are at the site of the membrane, of extra large size, both in dermal and epidermal layers.

In embryo 'Q' (figs. 8 *a*, *b*, *c*) the further growth of the membrane is shown. In the more anterior sections the membrane has not appeared, and the lower lid is thick and rounded; further back the sections show the membrane as a thin tongue of epiblast-clad dermis springing from the ocular edge of the lower lid. More posteriorly the method of deepening of the sulcus between membrane and lid appears, the epidermis penetrates the cleaving dermis as a double row of cells whose contiguous surfaces are as yet unseparated by any formation of cuticle.

In embryo 'R' (figs. 9 *a*, *b*) the membrane now projects from the ocular surface of the lower lid to a considerable extent, and the covered part is separated from the lower lid by a fissure, penetrated by epiblast, of a depth equal to two-thirds the length of the projecting portion of the membrane.

In later embryos up to 'full-time' the position and form of the membrane has been observed, and it is to be noted that at no date is there any tendency to that union of the upper and lower eyelids which forms permanently in reptiles and temporarily in mammals (Donders, 8, p. 291).

*The conclusion I would draw from these observations is, that the growth of epiblast-clad dermis which constitutes the membrana nictitans arises from the ocular surface of a previously formed lower lid.*

Of the sections reproduced, those numbered 7 c, 8 c, and 9 b, are taken through that part of the bulb in which the posterior part of the optic nerve appears, so that the sections represent as nearly as possible the same level, and by comparison the rate of growth can be observed.

#### 6. *The Development of the Musculature of the Membrane.*

Although the musculature of these structures would seem somewhat complicated from the many names attached thereto, yet examination of their connections shows that there is no one muscle which is independent of another; all are more or less closely connected or continuous with the other muscles of the membrane or of the spiracle.

The latest description, by Ridewood, recognises the following muscles in this region:—

1. *Levator palpebræ nictitantis.*
2. *Depressor palpebræ superioris.*
3. *Retractor palpebræ superioris.*
4. *Constrictor spiraculi.*
5. *Dilator spiraculi.*

With this differentiation my own dissections agree, and in referring to the muscles I shall adhere to this nomenclature.

These five muscles appear from the gross anatomy to constitute two sets only, a superficial and a deep.

The first or superficial set appears to comprise the *retractor palpebræ superioris* and the *constrictor spiraculi*. Ridewood suggests their origin may be from "a purely dermal system of muscles." The unity of the *levator palpebræ nictitantis* and *dilator spiraculi* is a most obvious one, and with these is closely associated in its origin the *depressor palpebræ superioris*. These constitute the deep muscle sheet, a view shared by Hubrecht (15, p. 100), Tiesing (32, p. 92), Allis (1, p. 571), and Ridewood; and, to quote the last named, they "would together represent that undifferentiated pre-spiracular muscle of *Heptanchus* which



Vetter has described as the *constrictor superficialis dorsalis*" (25, p. 242).

In the earliest of the *Mustelus* embryos, 'N,' sections through the middle of the branchial plate immediately in front of the anterior limb-bud show the state of the development of the musculature of the region (fig. 10). The muscle plates are represented by two crescentic masses lying on each side lateral to the neural canal and notochord, and extending ventrally by two partially separated blocks of tissue into line with the dorsal aorta. Dorsally, the plates of each side are separated by a considerable interval, and within the cells forming the extremities there yet remains the cavity of the myotome. The protoplasm of the cells of the main masses is increasing in quantity, and the cells show a radial arrangement from the centre to the periphery. Two small masses of muscle-cells appear in the mesoblast, on each side ventro-lateral to the heart bulge; these in the lower sections can be traced into connection with the muscle plate. Besides these masses there is seen the muscle of the branchial bar, which appears as a mass of spindle-shaped cells lying lateral to the cardinal vein, and much nearer to the dermis than the muscle plate. Passing ventrally, this mass divides into two parts, a larger extending superficially to the dorsal invagination of the gill pouch and into the branchial bar, and a smaller, deeper part which penetrates between the dorsal invagination of the gill pouch and the cardinal vein. A comparison of these and more posterior sections shows that the relation of the anlage of these branchial muscles to the dermis and muscle plate differs from that borne by the anlage of the limb muscles to these structures. The latter can be traced into direct connection with the ventro-lateral extension of the muscle plate, whilst the branchial muscle has a much closer connection with the mesoblast of the dermis than with that of the muscle plate. This is especially the case in sections through higher regions.

Tracing these muscle masses upwards, it is found that in the sections immediately posterior to the auditory epiblast the muscle plate is not seen, but the branchial muscle anlage can be traced until the region posterior to the eye is reached.

In the second embryo, 'P,' the muscle plate has given place








to a dorsal musculature arranged in a characteristically laminated and symmetrical fashion. The branchial muscles have increased in size, the deeper part to the greater extent; the connection of the deep part with the branchial cartilages is distinct, whilst the superficial can in parts be traced into a ventro-lateral extension. The connection of the conjoined dorsal extremity of both superficial and deep portions with the superficial dermis is more pronounced. The dorsal musculature has now extended over the auditory invagination for some distance; but, occupying a position still anterior to this, the branchial muscle can be traced; it forms two parts, a small superficial mass of cells lying beneath the surface epiblast in close connection with the roof of the spiracle, beyond which it cannot be traced, and a deeper portion which is more differentiated as muscle tissue, and can be traced, anteriorly to the spiracle, into connection with the maxillary cartilage. In the hinder sections both these portions unite in the dorsal region.

In the fourth embryo, 'R,' the state of the general muscular development shows a considerable advance on the former. As regards the spiracle region, the same masses of muscle described in the previous paragraph are to be seen. From a common mass situated dorso-lateral to the spur of the auditory capsule (fig. 11) they separate out as a maxillary mass and a spiracular mass (fig. 12); the former passes to the maxillary cartilage and the latter to the skin in the region of the spiracle. Besides these masses there is a new and third mass which appears first in the region of the branchial bar, which is the second after the spiracle, as a thin streak of cells lying in the superficial mesoblast of the dorso-lateral region (fig. 11); tracing this forwards, it is found to become shorter and thicker and more definite, until nearing the spiracle it forms a sharply defined mass of cells of small size, closely applied to the angle formed between the roof of the spiracle and the skin. A few sections further forwards the other spiracular mass separates from the maxillary mass and blends with this third mass, and the two make a single mass of considerable size upon the roof of the spiracle (fig. 12). A part of this mass remains closely applied to the skin after the spiracle has been passed (fig. 13), when it becomes elongated and extends somewhat ventrally; later it separates into two portions, a

large ventral and a smaller dorsal portion, which are lost in the skin-fold covering the posterior angle of the ocular cavity at two spots, from which a few sections further forward there arise the upper and lower lid-folds (fig. 14).

To summarise the description of the musculature of these embryos, it may be said that the branchial muscles arise in the dermal tissue at some distance from the muscle plate, these pass as two divisions, superficial and deep in their relations to the dorsal pouch of the gill slit, and that there can be traced in the region of the higher arches the origin of a yet more superficial musculature within the most superficial layer of the dermis. Further, that a like origin can be found for the muscles of the spiracle region; of these the deepest portion is seen to be connected peripherally with the maxillary cartilage, and the two superficial sets with the spiracle walls and the contiguous skin.<sup>1</sup> And lastly, that in the latest embryo parts of these two superficial muscle masses can be traced anteriorly beyond the spiracle into the eyelid folds.

The proportion existing between the state of the spiracle and its muscles in the adult Plagiostomata, and the degree of development of the nictitating membrane and its musculature is striking. It is in an inverse ratio. What may be the determining factor of this relation I am unable to suggest.

| Species.            | Spiracle.   | Spiracle Muscles.   | Nictitating Membrane.   | Muscle to Lids.   |
|---------------------|---|---|---|---|
| Rays, . . .         | very large  | distinct  | none  | none  |
| Rhina, . . .        | do.   | do.   | do.   | do.   |
| Acanthias, .        |  |  | do.   | simple retractors   |
| Scoyllium, . .      |   |   | simple fold   |  |
| Mustelus, . .       |   |   |  |  |
| Galeus, . . .       | very small  |   |   |   |
| Carcharias Zygaena, | absent  | traces only   | perfect   | large and complex   |

<sup>1</sup> This derivation of branchial and spiracular musculature from homologous sources confirms the homologies given for these systems by Vetter (34, p. 407, et seq.).

The close relation which spiracle and eyelids have in the embryo and young fish is not apparent from examination of adult species; in the latter, growth has separated the two considerably. A comparison of the measurements of the shortest distance between the palpebral fissure and the spiracle to the length of the palpebral fissure will illustrate this. The proportion is shown in an index giving the ratio of palpebral-spiracle distance to the palpebral fissure length taken as 100 :—

| Fish.                 | Length of Fish. | Palp. Fissure. | Palp. Fiss. to Spiracle. | Index of Approximation. |
|-----------------------|-----------------|----------------|--------------------------|-------------------------|
| <i>Galus</i> (adult)  | about 1000 mm.  | 35 mm.         | 25 mm.                   | 71                      |
| <i>Mustelus</i> (do.) | „ 700 „         | 25 „           | 10 „                     | 40                      |
| „ (embryo)            | „ 260 „         | 12 „           | 1.5 „                    | 13                      |
| „ (do.)               | „ 200 „         | 8 „            | 1 „                      | 12                      |
| „ (do.)               | „ 70 „          | 5 „            | 0.5 „                    | 10                      |

Regarding the ultimate source of origin of the muscle masses above described, the relation which the ordinary branchial muscle anlagen are found to bear to the dermis is the same as that generally accepted. This dermal tissue has been shown to be the derivative of the outer layer of the myotome, so their source is that common to all muscle tissue, but the indirectness of their connection indicates an evolution antecedent to such muscle tissue as that of the limb-buds where the derivation is a direct one. Of the presence of the most superficial mass of muscle tissue arising within the superficial dermis in the higher branchial segments (figs. 11 and 12, *m.s.s.*), I can find no record of previous observations. In time of origin it is later than the other branchial musculature, but its dermal source, since it is the more superficial, indicates an origin from an earlier dermal outgrowth from the myotome, but whether this will show the morphological value of the muscle as of primitive or later evolution I am unable to determine.

*The conclusion of these observations is that the musculature of the eyelids of Mustelus is derived from a musculature primarily belonging to the spiracle; also that there is evidence to show that*

*this arises from two original sources,—the one a superficial dermal layer, the other a portion of a deeper dermal muscle layer.*

### *7. The Nerve Supply of the Musculature.*

Previous to my dissections of the adult fishes in Easter 1898 at the Plymouth Laboratory, I had read the statement that the muscles of the membrana nictitans were supplied by the N. abducens—Huxley (17, p. 67), Staunius (30, p. 163). In dissecting out the connections in *Mustelus*, and later in *Galeus*, I was able to trace the whole of this nerve into the M. rectus externus, and to note the origin of the 'nervus nictitans' from the maxillo-mandibular division of the N. trigeminus. This observation I communicated then to Mr Holt (hon. naturalist to the M. B. Assn.), and a few days later to Professor Macalister. Ridewood gives this origin for the nerve in his paper. Since then I have repeated the dissection with the same result.

The N. abducens escapes from the skull by the same foramen as the N. trigeminus, and is bound up in the same tough fibrous sheath; it enters the substance of the M. rectus externus immediately on leaving the foramen, so that it does not appear exposed in the orbital cavity, and the muscle must be opened out before the nerve can be seen. The N. abducens was separated from the N. trigeminus in its entire course, and found to be entirely free from connection with the N. nictitans. The origin of this nerve was traced into the trigeminal, and in its substance through the cranial foramen. Beyond this I could not follow it.

In embryo 'R' I have traced the nerve from the periphery along the posterior orbital wall to its connection with a portion of the N. trigeminus trunk close to the Gasserian ganglion. This part of the trunk, on being traced peripherally, gave origin to the nerve of supply to the M. levator maxillæ superioris.

In embryo 'N' the same tracing could be followed to the inner side of the ganglion, and the connection appeared to be continued from here to the medulla through the ventral part of the root. I give these observations with due reserve, for it is very difficult to feel sure that one is following the same small group of neurons through many transverse sections, when the

group is contiguous with or surrounded by neurons of an exactly similar character. The difficulty was recognised by Balfour (4, p. 197).

That the N. nictitans has no connection with the N. abducens I am well assured, but I could not eliminate the possibility of a connection with the N. facialis, which in the embryo is situated in close connection with the ventral root of the N. trigeminus, and it seems likely that the ultimate source of the nerve may be from the N. facialis. The close connection which these two cranial nerves make in their origin is well shown in the schematic figures of longitudinal sections of *Scyllium* embryos in stages 'L' and 'N,' by Marshall and Spencer (21, pl. xxvii. figs. 10 and 11). Also, on this point the observations of Stannius on the cranial nerves of Plagiostomes may be quoted (31, p. 30). In Plagiostomes, N. trigeminus and facialis arise conjointly from three roots, the most anterior of which arises from the ventral surface of the medulla by two short roots, which unite shortly after leaving the brain. This root is in *Raja* mainly the motor-supply of the muscles by which the respiratory movements of the anterior wall of the spiracle are effected, and also of certain other muscles in connection with the jaws. Ewart (9, p. 529), on the nerves of *Lamargus*, describes the origin of the nerves supplying the muscles in front of the spiracle, from the mandibular division of the trigeminal, and later notes the close connection of part of the facial complex with this nerve. These observations on the nerve supply of the spiracle muscles are significant, in view of the origin of the musculature of the eyelids from these muscles, as I have shown above.

#### 8. *The Outer Corneal Layer.*

In the descriptions of the simpler forms of palpebral apparatus, I have frequently referred to the above-named structure in connection with the bulbar attachment of the conjunctiva. In a very large number of species, by incising the skin immediately around the bulb, there can be stripped off a thin layer of transparent 'skin' from the front surface of the bulb. It is always attached to the remaining or bulbar part of the cornea,

to a greater or lesser degree, by delicate connective tissue which can be seen tearing up as the flap is pulled off. In some fishes the connection is so slender that the separation can be made and the 'space' injected by forcing fluid through a hole made in the outer layer, when it will be demonstrated that the 'space' has no connection with other subcutaneous tissue. In diseased conditions of captive fish this potential 'space' frequently becomes actual and distended with gas; a like condition may affect loose tissues elsewhere. I have seen a similar condition in freshly caught Pouter-whittings, and I am informed that this is always the condition of this fish immediately on removal from the water, but there is no appearance of it in the healthy free-swimming fish.

In Eels the layer is removable with some difficulty, and then the bulbar part of the cornea can be stripped off layer by layer of transparent connective tissue.

The outer corneal layer is separable in almost every species of sea-fish, excepting those of voracious habits. It is not separable in those whose habitat is fresh or fresh and salt water, thus:—

It is inseparable in Selachoidei, Batoidei, Holocephala, Chondrostei, Perciformes, Cotto-scombriformes (ex. Lophius), Mugiliformes, Cyprinina, Esocidæ, Salmonidæ (ex. Smelt), and Clupeidæ.

It is separable in Gastroteiformes, Gadoidei, Pleuronectoidei, Murænidæ, Syngnathidæ, and Gymnodontes.

The only exceptions to the generalisation from habitat are Smelt and Stickleback. Both these fish were very small and soft, being winter specimens, so that the exception may be accounted for by ill-condition. The Eels appear exceptions, but the remark on the mode of separation for these fish shows them to be on the border line. The histology of the cornea in Cod, Eel, and Trout has been treated by Lightbody (20, p. 40), who shows there is in Cod a layer of muco-areolar tissue dividing the cornea into two parts. I have made similar observations on the Plaice, which show that the proper substance of the cornea is not completely organised.

## II. RELATION OF BULB TO ORBITAL WALLS.

1. *The Orbital Sac* (fig. 16).

On opening the orbital cavity of a fish by an incision through the skin of the lower eyelid or palpebral margin, the cavity will be seen in most species to present the appearance of a large lymph sac containing a small quantity of pale straw-coloured fluid. Into the cavity projects the bulb, and across it stretch the bulbar muscles and nerves. The cavity is lined by a membrane which is reflected over the walls of the orbit, the bulb and the structures connected therewith, thus forming visceral and parietal reflections of the sac. It may extend from the region of the optic foramen to the cul-de-sac produced by the union of the conjunctiva and the outer corneal layer, and arising from below the bulb it tends to enfold bulb and muscles, and to meet above these structures. It can be found in a small but sharply defined state in the Angler, where an incision below the eye will give entrance to a smooth and thick walled bursal-sac which turns up slightly before and behind the bulb; the special features of the sac found in this fish show an excellent adaptation for the service of the eye, which needs to be protected from the action of the huge subjacent pharyngeal muscles during the spasmodic working of the trap-like jaws. In the Salmon and Ling the sac is larger, the visceral layer forming a funnel-like investment to the bulb and its muscles. In other fish this layer has become more discrete, affording separate investments to each of the muscles. Such a condition is found in the Pleuronectids.

2. *The Recessus orbitalis*.

In these fishes the sac is unusually large, and has in connection with it a reticulated muscular diverticulum, which lies without the orbital wall posteriorly, and between the mandible muscles and the dorso-lateral skin. It has been described by Holt (14, p. 422) as the recessus orbitalis. I have found the recessus according with the description given in all the species of the fishes I have examined, which include a few beyond those named by Holt. I have further attempted to determine the

nerve supply of the recessus. By ordinary dissection no more can be ascertained than that the structure is crossed by two slender branches of the N. trigeminus, as stated by Holt; so the examination was continued in two ways, experimental and histological.

By the courtesy of the officials of the Brighton Aquarium, I was able to stimulate the nerves of the region in a freshly killed plaice. A Dubois Reymond coil and platinum electrodes were used, and the effects of the current in single, slowly repeated and rapid induced shocks observed, after testing the current on the ordinary skeletal muscles with satisfactory effects. These methods were used on the branches of the N. trigeminus in relation to the recessus, on the blood-vessels supplying the saccus, in the hopes of stimulating sympathetic fibres, and lastly on the recessus itself, but in each case the result was negative.

Further, portions of the fresh recessus were treated by Dogiel's methylene blue and Löwit's gold chloride methods for tracing nerve endings. By both these means of preparation several fine nerve fibres could be followed in their course within the elastic outer coat of the recessus; these nerves arose from the N. trigeminus, and in one case there was an appearance of short thin twigs given off at right angles to one of these fine nerve branches to end in the underlying muscle tissue, but this was seen in only one gold preparation, and in only a small part of that, so that without repetition it cannot be accepted as evidence of the manner of the nerve ending. The blood-vessels make a very complete network in the elastic coat. The muscles can be seen arising from the proximal portion of the recessus as fasciculi, which give off many branches to connect with neighbouring fasciculi; at the periphery of the recessus many slender branches arch over to connect with similar branches from the other side.

I have not yet succeeded in tracing the origin of the recessus from the orbital sac. The origin of the latter can be clearly followed in the *Mustelus* embryos (fig. 7c). It arises by a simple cleavage of the mesoblast packing which fills the interval between the developing optic capsule and cranial walls; it is therefore analogous in its formation to the other greater connective-tissue spaces of the body.



### 3. *The Capsule of Tenon* (fig. 16).

Within the visceral layer of the orbital sac, and separating it from the sclerotic, is a fibrous capsular investment to the bulb. I have applied the above name to it since the capsule corresponds very well to the ocular investment known by this name in the higher mammalian anatomy. It is separated from the osseous, cartilaginous, or fibrous sclerotic by loose connective tissue, which may contain more or less mucous tissue. It is united with the fibrous sheath of the optic nerve near the entrance of the latter into the bulb, and it blends with the tissue of the palpebral margin or lids and that of the subconjunctival region. Each bulbar muscle receives an investment which extends in the direction of the origin of the muscle. Langhans (18) and Owen (24, p. 334) include this in the tissue of the sclerotic, but I think the relation which it bears to the bulbar muscles is sufficient to separate it from the true sclerotic. The capsule, however, can hardly be considered to perform the pulley-like action for the muscles, ascribed to the like investment in man, except in the case of pleuronectids (*infra*, Section III. 3), since the sclerotic is so stiff as to need no protection from muscle pressure. In one species the capsular investments are peculiarly strong, to the detriment of the muscles; in the Conger the muscles are small and obscured by the dense white membrane covering them. This fact, together with the absence of conjunctival fornices, and the density of the skin connecting the cornea with its surroundings, accounts for the immobility of the eye. A captive specimen of this creature spends most of its time reposing in the shade of some drain-pipe provided for its delectation, or with its nose deep in some corner; any motion required for the extension of its vision appears to be supplied by the movements of its flexuous body.

In certain fishes the capsule comes into special prominence in connection with a structure, the—

### 4. '*Cartilago sustentaculum oculi*' (figs. 15 and 16).

The rod of cartilage to which I apply this name has been noticed by many observers. Sömmerring (29) names the earlier of these observers, and himself briefly describes the cartilages

found in *Raja* and *Acanthias*, and figures the excised eyes of these fish with the cartilages attached. Its presence in most Plagiostomata has been noted by Owen (24, p. 337), Günther (10, p. 112), and incidentally by Leuckart (19, p. 167), and Ruge (28, p. 243). Each has applied some loosely descriptive name such as 'Cartilaginous peduncle,' 'Augenstiel,' and 'Knorpelstab.'

The variations in its form in adult rays and sharks can be best illustrated by reference to the following fishes:—

The Blond Ray (fig. 15) shows it in its highest development as a broad flat cartilaginous rod which springs from the depth of a small depression of the cranial wall, and passes outwards and upwards in a gentle curve to end in a cup-shaped enlargement which is within the capsule of Tenon. This cup articulates with a semicircular enlargement of the bulbar cartilage, the whole forming a well developed cup-and-ball joint. In this fish the cup end of the cartilage is stayed by three fibrous strands which are affixed to the anterior and posterior orbital walls, and to the mesial wall at the posterior edge of the optic foramen. In *Acanthias* the cartilage is long, slender, and cylindrical, and the cup small; the relations to the bulb and Tenon's capsule are the same, but there is no special bulge on the bulbar surface for the articulation, also there are no ligamentous stays to the stem stretching across the orbital cavity; there is, however, a radial arrangement of strengthening fibres in the capsule, passing from the stem to the periphery of the capsule. In *Galeus* (fig. 16) the stem bears the same relation to the cranial wall and the capsule; the bulbar end is, however, not cup-shaped, but presents a plain smooth-surfaced knob, which is separated from the sclerotic by a pad of soft muco-areolar tissue. In *Mustelus* the cartilage is yet more reduced, and its connections with both cranium and capsule so fragile that it is displaced on the slightest manipulation.

In *Zygæna* the central end does not reach the cranium, but abuts on the common tendon of origin of the recti muscles (see Section III. 1). It is not found in *Scyllium*.

In all these cases the relation borne by the cartilage to the optic nerve is the same; the cartilage is posterior and slightly dorsal to the nerve, and separated from it at its central end by a considerable interval.

The uses which such an ocular support subserve are fairly obvious in the Skate, in which fish the eye is held at a level considerably above that of the surrounding skin. Apparently the fish has no power of altering the elevation of the eye, but the liability to risk of injury from slight violence, consequent on the projection, is minimised by the flattening of the upper surface of the bulb, and the cartilage, though hyaline, is sufficiently elastic to allow of depression with greater force.

In Sharks the cartilage compensates for the lack of support afforded the bulb by the unusually large size of the orbital cavity, and also appears to facilitate rapid and long continued bulbar movements. In watching a captive *Acanthias*, it was observed that with each stroke of the tail in swimming the head was deflected, whilst the eyes made a reverse and compensatory swing to maintain the constancy of vision.

The obliquity of the position of the cartilage obviates the defects to which inelastic support is liable.

*Development.*—The mesoblast is known to condense around the optic evagination, and one would suppose this cartilage to be developed in a portion of the mesoblast which surrounded the optic nerve and the distance between nerve and cartilage in the adult to be a result of separation by intercallary growth of the orbital wall; reference to the embryo, however, shows this is not the case.

In the earliest embryo there is no orbital sac; the small interval between the relatively large bulb and the condensing mesoblast of the skull is filled up by the growing orbital muscles and nerves, together with a quantity of loose mesoblastic tissue. In embryo 'P' (fig. 7c) the mesoblast becomes vacuolated in portions of the orbital cavity, whilst at a spot removed from the site of the optic nerve, by a considerable distance in a dorso-posterior direction, the mesoblast forms a denser band which connects the forming skull wall with the condensing optic capsule; within this mass cartilage is found in embryo 'Q.' Even at this early date the site of the connection of the anlage of the cartilage with the cranial wall is depressed, and it is from the bottom of this depression the column of mesoblast springs. Thus the cartilage has an origin independent of the immediate mesoblastic investment of the optic nerve, and seems to arise at

a situation where the bulb and orbit are in longest and least obstructed contiguity.

##### 5. *The 'ligamentum tenaculum oculi.'*

A fibrous band attaching the bulb to the mesial wall has been noted by Sömmerring (29, p. 70), Owen (24, p. 337), Günther (10, p. 112), and Leuckart (19, p. 169). In the majority of cases in which I have found the ligament present, it has formed a cord of variable strength lying anterior and parallel to the optic nerve, so that it differs in position from the sustentacular cartilage. It is present in this form in all freshwater fishes, *e.g.*, Pike, Tench, Carp, Trout, Bream, Perch; also in fishes frequenting salt and fresh water, as Salmon, Sturgeon, Herrings, Bass. It is present in a few only of the sea fishes, and these are Red Mullet, Mackerel, Tunny-fish, Grey Mullet.

The ligament in the Sea-bream (fig. 17) is noticeable in that it is separated from the optic nerve in its central attachment. The strong short fibrous cord of each eye springs from the same spot on the membranous interorbital septum, which is strengthened by a patch of dense white-fibrous tissue; the attachment to the bulb is, as usual, anterior and superior to the entrance of the optic nerve. In the Pike the ligament is very strong, Leuckart (19, p. 169) describes it as a slender elastic cartilaginous bar; I find it consists of a strong fibrous tube, within which is some soft glassy-looking material. Microscopical sections of the hardened ligament prove this to be merely muco-areolar tissue, and no trace of cartilage cells are to be found within it or the surrounding fibrous sheath; the strength of the structure lies in the fibrous outer part, so that it is essentially the same as the ligament of other fish. In the Rudd and Roach the ligament is double, for a narrower band lies posterior to the nerve in addition to the usual anterior ligament; the two meet in a web, and are attached to the bulb immediately above the optic nerve.

Regarding the origin of this ligament, I have made no observations on embryos, but I think that it will differ from that of the sustentacular cartilage in being merely a thickening of the mesoblast around the optic stalk, and not a separate growth, as

is the cartilage; this suggestion is supported by the presence of the ligament parallel to the optic nerve, in addition to the cartilage, in the case of the Ray (fig. 15).

### III. THE OCULO-MOTOR MUSCLES.

#### 1. General Scheme.

Within the large range of fishes examined the arrangements of the ocular muscles are singularly simple and regular; they consist of the usual *musculi recti* and *musculi obliqui*, and it is in but few species that variations in the shape and mode of attachment can be found.

As regards the origin of these muscles, the *M. recti* arise in most cases in immediate relation to the optic foramen at the posterior part of the orbit, and the *M. obliqui* from the anterior portion close to each other. The relations and variations of the origins in Plagiostomata are shown in the figures of Tiesing (32, *tab. v.*), and the connections for bony fishes are described by Stannius (30, pp. 59 and 174).

The variations from these plans are few. In *Chimaera monstrosa* there is, as noted by Gegenbaur (9a, p. 942), a displacement of the origin of the *M. rectus internus*, the muscle is much shorter than usual, and arises from the posterior edge of the frontal cartilage immediately in front of the membranous inter-orbital septum; it is supplied from the third nerve (Cole, 6, p. 642, and plate i.) by a long branch which passes over the optic nerve and across the interorbital septum to the muscle origin.

The origin of the *M. recti* of *Zygaena malleus* is described by Owen (24, p. 336) in the following terms: they "are remarkable for their length, since they arise from the basis cranii and extend along the lateral processes of peduncles, at the free extremities of which the eyeballs are situated"; a similar statement is made by Günther (10, p. 112). In the specimen of the fish which I dissected (spirit specimen, length 52 cm.), this was certainly not the arrangement found (fig. 18). On removing the skin from the inferior aspect of the lateral processes, the long strap-like optic nerve was seen; pulling this aside, there was exposed on its deep surface a fibrous band extending, in company with the

oculo-motor nerves, from the basis cranii to within a short distance of the bulb; from this band there arose by a common tendon the four recti, which were no longer than those found in other sharks of the same size;<sup>1</sup> between the common tendon and the bulb there was the usual sustentacular cartilage. The measurements of the muscles were:—

| Length of Fish. | Length of Lateral Process. | Length of Cranio-Muscular Ligament. | Length of Muscles, average. | Length of N. Opticus. |
|-----------------|----------------------------|-------------------------------------|-----------------------------|-----------------------|
| 520 mm.         | 50 mm.                     | 32 mm.                              | 14 mm.                      | 40 mm.                |

The insertions of the muscles vary within certain narrow limits. The usual method is by a thin flat tendon to the peripheral edge of the sclerotic. The M. rectus internus falls short of this attachment in Herrings and in the Salmon *Argentina silus* (the irregularity is not found in the common salmon or trout). In these fish the muscle is short and attached to the posterior pole of the bulb immediately anterior to the optic nerve; in all these cases the bulb is large, and fills the orbit very completely, so that the shortening may be the effect of pressure.

The relation which the insertions of the M. recti et obliqui superiores make with each other varies in form. In the Plagiostomata the muscles approach from the opposite angles of the orbit, and are inserted V-fashion into the sclerotic, their tendons being separated by a small interval; in other fish, Chimæra, Sturgeon, Caranx, Cantharus, Tunny, Perch, Hake, Roach, and Brama, the meeting is complete as a V-shaped insertion; in yet others the M. obliquus superior overlaps the M. rectus superior, as in the John Dory (figs. 17 and 19), and Sea-bream, Red Mullet, Cod, Ling, Tench, Rudd, Salmon, and Sun-fish; this progression increases until a complete crossing results, a condition found in Mackerel, Grey Mullet, Whiting, Haddock, and Little

<sup>1</sup> In re-examining Müller's figure of the dissection of the nictitating membrane of this fish (23), I find that this arrangement is indicated therein. No description is attached.

Pipe-fish. A similar relationship is found for the inferior muscles.

In some fish there is an intimate connection of the muscle-sheath, and even part of its tendon, with the subconjunctival tissue, as in the case of the *M. rectus externus* of Ling and all Pleuronectids. This tendency to form palpebral-retractor muscles is seen at its maximum in *Orthogoriscus*, an excised eye of which fish I have examined; the eye is of enormous size, the bulb being about the size of a closed fist, and each muscle a thick fleshy strap, having dimensions about  $15 \times 4 \times 2$  cm.; the mass of the *M. rectus superior* passes under the oblique muscle to its bulbar insertion, but a small part, superficial and anterior in position, passes on to blend with a detached superficial set of fibres of the oblique muscle; these conjoined fibres are then inserted into the tissue beneath the conjunctival. I am unable to give their relation to palpebral folds, if such exist, as the eye was too closely excised. A like relation exists in the *M. recti et obliqui inferiores*; the *M. rectus internus* also divides and is inserted in a similar double fashion, but no division appears for the *M. rectus externus*, though the connection of its tendon with the conjunctiva is close.

The description of the variation in the muscles of *Pleuronectes* is reserved for Section III. 3, of this paper, and remarks on the musculature of the Lamprey are reserved for a later paper.

## 2. *Variations for Projection and Retraction.*

In certain fish whose bodies have become much flattened laterally, whilst they still retain the dorso-ventral position normal to fish, there are effects arising out of the relation of the muscles to the bulb which can produce projection of the bulb. In watching the movements of a captive *Zeus faber*, it appeared that the fish had the power of projecting outwards the bulb, especially in the posterior quadrant, so increasing its range of vision nasal-wards. Dissection of a specimen showed that there was no special apparatus whereby this could be performed, but that the *M. rectus internus* was unusually long, and that the position of the muscle in its passage from the sub-cranial canal along the mesial aspect of the discoid bulb to its



insertion was such that a contraction of the muscle must result in the movement of the bulb in an outward direction (fig. 19), any substantial internal rectification such as could be effected in a more spheroidal eye, being prevented by the coincident pressure of the bulb against the long strap-like muscle and the posterior ocular wall. In this case the short *M. rectus externus* would act as a retractor.

The eye of *Periophthalmos* is credited with the movements of projection and retraction. Günther (10, p. 488) writes:—"The peculiar construction of their eyes, which are very movable, and can be thrust out of their sockets, enable them to see in the air as well as in the water; when the eyes are retracted they are protected by a membranous eyelid." I have had no opportunity of observing the movements of the living fish, but have examined and dissected a small spirit specimen. The large round eyes were raised freely from the lateral surface and above the level of the dorsal osseous crest; their appearance of isolation from their surroundings was heightened by the presence of a deep sulcus existing between the bulb and the subjacent bulge of the maxillary muscles; no eyelid formation was visible, the surrounding skin formed a collar of soft tissue which was probably loose in the fresh state. A wide circular incision allowed the whole of the skin of the side of the head with the bulbar skin collar and the outer corneal layer to be removed with ease, and no part of the removed skin showed any special thickening, as would be necessary for the formation of a 'membranous eyelid.' The exposed orbital cavity was roomy and completely lined by the orbital sac, which extended between the skin of the infraorbital sulcus, above described, and the upper surface of the maxillary muscles. No contractile or elastic part of the sac, such as the recessus orbitalis, could be found; but I must here repeat, the specimen was small. The muscles were normal, except for the relation of the *M. rectus et obliquus inferiores*: these crossed each other in their mid-lengths, the obliquus being the superficial.

My impression from the examination of this specimen is that the special motion of the eyes of this fish must be a *vertical elevation and depression* rather than projection and retraction. In the deep and wide infraorbital sulcus, the extent of which is



not indicated in the figure attached to Günther's description, there exists a provision which would allow of considerable depression of the bulb in the flaccid state of its muscles, whilst the position of their orbital attachments and the 'cradle' formed by the crossing of the inferior muscles are such that general contraction of the muscles, to even a moderate degree, would elevate the bulb from its resting-place.

The above examples, and that of the Pleuronectid fishes (*vide* 'orbital sac' and *infra*), are the only cases in which projection and allied motions could be found. Occasionally, in handling fish preparatory to killing them, I have noticed a decided retraction of the eye: this has been mostly in freshwater fish, *e.g.* Pike and Tench, but I have seen no such effects in swimming captive specimens.

### 3. *Modifications in Pleuronectid Fishes.*

Observations of the eye movements of captive specimens of these fishes will show that, beyond the power of projection described by Holt, there is a distinct power of *rotation* of the eyes,—a power which I think is peculiar to them, and one which probably depends upon a secondary adaptation of the eye muscles to their habits of life. The eyes can be moved around a central axis, passing through the cornea to the posterior pole of the bulb, and the rotatory excursion may extend to as much as one-eighth of a circle. This peculiarity of motion is amply accounted for by a specialisation of the M. obliquus superior, a muscle which in these fishes is of unusually large size relatively to the others.

I shall describe the arrangements of the muscles in the Halibut, a convenient fish on account of the great size of its eye muscles (fig. 20). The M. obliquus superior takes origin from the anterior angle of the orbit, and passing outwards to the bulb in the direction of the usual site of insertion, it now enters an investment of Tenon's capsule and divides into two parts. The larger is inserted by a thin flat tendon into the sclerotic just behind the sclero-corneal junction, and in close connection with the tendon of the M. rectus superior; the smaller portion, after leaving the main mass, crosses the M. rectus superior, and

lying within a sheath derived from Tenon's capsule, it follows the posterior quadrant of the bulb until reaching the level of the *M. rectus externus*, where it is inserted by a thin tendon into the bulb on the line of its greatest circumference immediately deep to that muscle. The slip is supplied from the *N. trochlearis* by a branch which separates from the main trunk before it reaches the muscle. This special slip is present in both eyes of all the species which I have been able to obtain, in both dextral and sinistral fish, and in both large and small specimens.

The degree of separation of the slip from the main oblique mass differs: it is more complete in the common Plaice than in the Halibut, still more so in the Rough Dab, and most in the Flounder, where the division extends for the greater part of the muscle length. In this fish the *M. obliquus superior* is more extended in its insertion, part of its fibres crossing the upper surface of the *M. rectus superior*. No such special arrangement is found in the inferior muscles, but the *M. obliquus* crosses the *M. rectus* superficially in a manner described for other fish; and in Turbot and Brill these muscles are so diminished in size that their insertion is by two small superimposed tendons immediately ventral to the optic nerve.

Cunningham (7, p. 50), in his monograph on the Sole, devotes considerable space to the eye muscles. He notes a disturbance of the origin of the oblique muscles of the displaced eye, and also the crossing of the inferior muscles near their insertion; but in his description of the *M. obliquus superior*, no mention is made of this special development.

It is evident that this specialisation of the *M. obliquus superior* is calculated to extend the field of vision in a manner peculiarly advantageous to a fish which, from its adoption of a sedentary life, will lose the range obtained by the rapid body movements of more active and free-swimming fish.

It is worthy remark in this connection that in those creatures whose eyes are situated laterally in the head, and have their visual axes lateral, the *M. obliqui* are simple in their character; but in creatures whose visual axes are capable of convergence, there is a specialisation of the *M. obliquus superior*. The direction of the visual axes of Pleuronectid fishes, in the projected

state of the eye during life, is frequently one of convergence: the eyes of many mammals are capable of rotating about convergent axes, *e.g.* the horse, and the condition is complete in man. In all these there is a specialisation of the *M. obliquus superior*, and broadly speaking along the same lines—one of extension of the muscle.

Regarding the *M. rectus externus* and *internus*, both of these are subject to some variation. In most of these fish there is a diminution in the size of the external muscle. In the Halibut it is a small rounded muscle, deficient in contractile substance for the distal third of its length, a great contrast to the broad strap-like appearance of the other muscles; the insertion is by a slender tendon which runs for some distance in a fibrous sheath, closely adherent to the subconjunctival tissue, to its insertion at the extreme edge of the sclerotic; some of its fibres pass into the subconjunctival tissue. This diminution was found to a greater or less degree in all the species examined. The causation is not clear; it may be due to a decrease coincident with increase of the anterior muscles to allow more freely of convergence; in some cases it seemed as though the hump caused by the mandible muscles obscured the range of vision posteriorly, and with this the smallness may be connected. In the case of the Rough Dab, this is undoubtedly connected with a partial displacement of other *M. recti*; the *M. rectus superior* is more posterior in insertion than usual, so as to be almost parallel with the *M. rectus externus*, thus sharing its action, whilst the *M. rectus internus* has become more superior than in others of the genus.

The following are the measurements of the muscles of a large Halibut and Turbot; the heads of the fish were of nearly full size, as is shown by the measurements taken from the symphysis of the mandible around the gill cover to its dorsal extremity. The smallness of the muscles of the Turbot and Brill, with the shortened insertion of the inferior muscles, and the feeble power of projection possessed by the latter fish, Holt (14, p. 429) appear to be correlated with the inelasticity and lack of volume in the circumcorneal skin collar.

*Measurements of Muscles (millimetres).*

| Fish.   | Jaw-gill length. | Superior Oblique. |                | R. Supr.    | R. Ints.   | R. Exts.   | R. Infr.    | Inf. Obliq. |
|---------|------------------|-------------------|----------------|-------------|------------|------------|-------------|-------------|
|         |                  | Main mass.        | Special Slip.  |             |            |            |             |             |
| Halibut | 370              | 43 × 20 × 4       | 40 × 4 × 2     | 84 × 11 × 4 | 85 × 8 × 5 | 81 × 5 × 8 | 80 × 13 × 3 | 39 × 12 × 4 |
| Turbot  | 228              | 28 × 4 × 1        | 16 × 1.5 × 0.5 | 43 × 4 × 2  | 44 × 3 × 2 | 46 × 1 × 1 | 36 × 4 × 2  | 20 × 4 × 2  |

In concluding, I wish to state my indebtedness to Dr Harmer, Curator of the Zoological Museum, Cambridge, for access to fish which could not be obtained by purchase; and to the Worshipful the Company of Fishmongers for their nomination to a table at the Plymouth Laboratory of the Marine Biological Association.

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## DESCRIPTION OF PLATES I.-VI.

Fig. 1. The "pseudo-membrana nictitans" of *Salmo salar*, dissected out. The broad ligament is the anterior. The curved groove on the surface is the impression of the anterior palpebral fold.  $\times \frac{1}{1}$ .

Fig. 2. The head of *Clupea harengus*, showing the three palpebral folds and narrow vertical palpebral fissure.  $\times \frac{1}{1}$ .

Figs. 3, 4, 5, and 6. The right eyes of (3) *Carcharias glaucus*, (4) *Galeus vulgaris*, (5) *Mustelus laevis*, and (6) *Scyllium canicula*. Figs. 3 and 6 are life size, 4 and 5  $\times \frac{1}{2}$ .

Figs. 7 a, b, c. Series of transverse sections through the lower palpebral apparatus of *Mustelus laevis* embryo 'P.'

Fig. 7c also shows the formation of the cartilago sustentaculum oculi (c.s.a.) and of the orbital sac (o.sc.).

Figs. 8 a, b, and c. Series of sections through the lower palpebral apparatus of *Mustelus* embryo 'Q.'

Figs. 9 a and b. Series through same structure of embryo 'R.'

Fig. 10. Transverse section through mid-pharyngeal region of *Mustelus* embryo 'N,' to show state of musculature. Shows position of branchial muscle (m.b.), with its portions superficial and deep to the dorsal gill pouch.

Fig. 11. Transverse section post-spiracular region, *Mustelus* embryo 'R,' showing musculature. Dorsal muscle (m.d.), the maxillo-spiracular muscle mass (m.m.s.), and the origin of the most superficial spiracular muscle tissue (m.s.s.).

Fig. 12. Transverse section through spiracle, same embryo, shows separation of maxillo-spiracular muscle mass into M. levator maxillæ (m.mx.), and M. spiraculi (m.sp.); also the union of the latter with the M. spiraculi superficialis (m.s.s.).

Fig. 13. Transverse section through præ-spiracular region, same embryo, shows continuation anteriorly of part of spiracle muscle mass, as musculature of eyelids (m.pp.). It can be seen to be composed of two strata of cells.

Fig. 14. Transverse section through posterior extremity of the orbit, same embryo. The palpebral muscle mass of the preceding section is seen to be divided into a small dorsal and a larger ventral masses situated within the palpebral margin; these can be further traced to the lids.

Fig. 15. View of the orbit of *Raja blanda*. The bulb is raised to show the cartilago sustentaculum oculi (c.s.) and its three ligaments, anterior l', internal l'', posterior l'''.  $\times \frac{2}{3}$ .

Fig. 16. Coronal section through orbit of *Galeus vulgaris*, at the posterior edge of the optic foramen (f.o.), shows orbital sac and its reflections (o.sc.r.). Tenon's capsule (T.c.), its sheathing evagination to M. rectus superior (T.c.s.). The M. rectus inferior is seen within the capsule (r.if.). The connection of the cartilago sustentaculum oculi (c.s.) with the capsule, and the muco-areolar pad (m.) which separates its bulbous end from the sclerotic. The section shows well the relations of the palpebræ and membrana nictitans to the conjunctival fornices.  $\times \frac{2}{3}$ .

Fig. 17. Dorsal view of dissection of left orbit of *Pagellus centrodontus*, to show ligamentum tenaculum oculi.  $\times \frac{1}{1}$ .

Fig. 18. Ventral view of head of *Zygæna malleus*, showing dissection of eye muscles. The N. opticus has been pulled aside to show the tendinous band (*t.b.*) from which arise the M. recti.  $\times \frac{1}{2}$ .

Fig. 19. Dorsal view of left orbit of *Zeus faber*, to show relation of M. rectus internum to discoid bulb to produce projection in direction of arrow.  $\times \frac{1}{1}$ .

Fig. 20. Dorsal view of right eye of *Rhombus maximus* with muscles attached; the extension of the recti into the subcranial canal is not indicated. To show form and position of the special rotatory slip of M. superior obliquus (*o.s.x.*).  $\times \frac{2}{3}$ .

*Scale of figures of microscopic sections.*

Scale 1, figure 7*a*, for figs. 7 *a*, *b*, 8 *a*, *b*, *c*, 9 *a*, *b*.

Scale 2, figure 10, for figs. 7*c* and 10.

Scale 3, figure 11, for figs. 11, 12, 13, and 14.

INDEX TO FIGURES.

*a.c.o.* anlage of optic capsule.

*ao.* aorta.

*b.b.* branchial bar.

*c.c.* cranial cavity.

*c.s.* cartilago sustentaculum oculi.

*c.s.a.* anlage of sustentaculum oculi.

*c.w.* cranial wall.

*f.o.* foramen opticum.

*g.s.* gill slit.

*ht.* heart.

*l.* lens.

*l', l'', l'''*. ligamentous strands to cartilago sustentaculum oculi,—  
anterior', internal'', and posterior'''.

*l.t.* ligamentum tenaculum oculi.

*m.* muco-areolar pad.

*m.b.* branchial muscle.

*m.d.* dorsal muscle.

*m.md.* m. levator mandibularis.

*m.m.n.* m. lev. palpebræ nictitantis.

*m.m.s.* maxillo-spiracular muscle mass.

*m.mx.* m. lev. maxillaris.

*m.p.* muscle plate.  
*m.p'* muscle plate ventral extension.  
*m.pp.* palpebral muscle mass.  
*m.ps.* muscle mass to upper lid.  
*m.sp.* do spiracle.  
*m.s.s.* superficial dermal muscle to spiracle.  
*m.t.* mucous tube.  
*md.* mandible.  
*md.c.* mandibular cartilage.  
*mx.c.* maxillary cartilage.

N. II. N. opticus.  
 N. III. N. oculo-motorius.  
 N. IV. N. patheticus.  
 N. V. N. trigeminus.  
 N.n. nasal branch of N. V.  
 N. X. N. pneumogastricus.

*o.c.* orbital cavity.  
*o.i.* m. obliquus inferior.  
*o.s.* m. obliquus superior.  
*o.s.x.* m. obliquus *special rotatory slip*.  
*o.sc.* orbital sac.  
*o.s.c.r.* reflection of orbital sac.  
*o.w.* membranous orbital wall.  
*ot.c.* otic capsule.

*p.a.* anterior palpebral margin.  
*p.e.* extra palpebral fold—'pseudo-membrana nictitans.'  
*p.f.* palpebral fornix.  
*p.i.* inferior palpebral fold.  
*p.m.n.* membrana nictitans.  
*p.p.* posterior palpebral margin.  
*p.r.g.* posterior root ganglion.  
*p.s.* superior palpebral fold.  
*ph.* pharynx.

*r.* retina.  
*r.e.* m. rectus externus.  
*r.if.* m. rectus inferior.  
*r.it.* m. rectus internus.  
*r.s.* m. rectus superior.

*sp.* spiracle.

*t.b.* tendinous band giving origin to m. recti of *Zygæna*.  
*T.c.* capsule of Tenon.  
*T.c.s.* muscular sheath derived from capsule of Tenon.

*v.* vitreous



THE JOINTS OF MAMMALS COMPARED WITH THOSE  
OF MAN: A COURSE OF LECTURES DELIVERED AT THE  
ROYAL COLLEGE OF SURGEONS OF ENGLAND. By F. G.  
PARSONS, F.R.C.S., *Hunterian Professor*.

MR PRESIDENT AND GENTLEMEN,—As I have the advantage of addressing an audience which is already thoroughly familiar with the anatomy of one mammal, Man, I propose to commence the description of each joint at the Primates, the order to which man belongs, and to work from these through the mammalian class to the Monotremata. In doing so I hope to lead you gradually from that which is better to that which is less well known.

THE TEMPORO-MAXILLARY JOINT.

It is unnecessary for me to review the chief characteristics of this joint in man; they will be drawn attention to when they contrast or agree with those of other animals.

In the monkeys, a flattening of the glenoid cavity caused by the more feeble development of the eminentia articularis is noticed, but while this boundary in front is diminished, the



FIG. 1.—Antero-posterior section through temporo-maxillary joint of Spider Monkey (*Ateles*).  $\alpha$ , post-glenoid process;  $\beta$ , condyle.

hinder one or post-glenoid process, which as a rule is feebly developed in man, is much enlarged, and an examination of the skull of almost any catarrhine monkey will show that this process is prominent only at the outer part of the back of the articulation. In the platyrrhine monkeys and lemurs the process is behind the centre instead of the outer part of the condyle, and

this change in the position of the post-glenoid process is coincident with a change in the direction of the long axis of the condyle. A comparison of the condyles of the mandible of a catarrhine monkey and a lemur will show that in the former the long axis is directed inwards and backwards as in man, while in the latter the long axis is quite transverse, and it has occurred to me that the lateral position of the post-glenoid process in the Catarrhini may have caused the obliquity of the condyle by stopping the outer part from moving backward while the inner part was still free to do so.

The meniscus of the Catarrhini naturally differs somewhat in shape from that of man, to adapt itself to the flatter glenoid cavity. Posteriorly it is attached to the front of the post-glenoid process, while in front it is connected with the anterior ligament of the capsule, which, when the jaw is retracted, lies horizontally and in contact with the anterior part of the glenoid cavity. The external part of the capsule in monkeys has the same backward and downward direction of its fibres as in man, but the function of them is different. In man, when the jaw is opened, the external lateral ligament is put upon the stretch, and I believe assists in the movement of the jaw forwards. In the monkey the condyle also moves forwards when the mouth is opened, but the external lateral ligament becomes less tense. It is quite certain that in either animal the forward movement of the condyle occurs in the cadaver when the mouth is opened, and is in no way necessarily dependent on the action of the external pterygoid muscle. I am at present engaged in some researches into the mechanism of this forward movement, and must defer a discussion on it to a later date.

In the Platyrrhini, the jaw joint differs little from that of the Catarrhini, except that the eminentia articularis is less well marked. In the Lemuroidea it has completely disappeared, but the post-glenoid process is well marked. The glenoid articular surface stretches forward for a great distance, but its transverse diameter is less anteriorly than posteriorly. The meniscus is flat above, concave below, and in my specimen was attached to the summit of the condyle by a delicate transverse fold of synovial membrane, which, however, was only present in the outer half of the joint.

In the fruit bat (*Pteropus*), which I examined as a type of the Cheiroptera, there is a very strong posterior ligament, but the external lateral is not particularly strong, and its fibres are vertical. On opening the joint it is seen that the temporal surface is quite flat; there is no post-glenoid process nor *eminentia articularis*. The condyle, on the other hand, is convex from before back, and elongated laterally as in man, consequently the meniscus is deeply concave below and flat



FIG. 2.—Antero-posterior section through temporo-maxillary joint of Fruit Bat (*Pteropus*).

above. The long axis of the condyle is quite transverse, as in the lemur. In the bat very little forward or backward movement of the condyle is allowed, and, as far as I can see, these movements are prevented solely by the very strong posterior ligament.

In the hedgehog (*Erinaceus*), an example of the Insectivora, the temporo-maxillary articulation closely resembles that of the bat; there is neither *eminentia articularis* nor post-glenoid process, but the condyle is not so convex antero-posteriorly, although it is transversely elongated.

In the Carnivora, as is well known, the joint is almost a perfect hinge; the transverse cylinder of the condyle is received into a glenoid cavity which fits it exactly, and consequently the meniscus is very thin. The cavity is bounded by the post-glenoid process behind, which is best marked internally, and the *eminentia articularis* or pre-glenoid process in front, which is most prominent externally. In the badger these two processes project so much that it is impossible to disarticulate the lower jaw without dividing it at the symphysis and drawing the two halves out sideways. In this animal, and indeed in most of the Carnivora, it would be impossible to open the

mouth were it not that the most prominent part of the post-glenoid process is quite at the inner part of the joint, and so clears the neck of the condyle. The pre-glenoid process, the homologue of the *eminentia articularis* of man, is very differently developed in different carnivores; it is especially well marked in the badger, otter, and glutton, but is hardly present in the paradoxure, skunk, ichneumon, bear, or fox. It is usually much larger in the *Felidæ* than in the *Canidæ*.

In the ruminant ungulates the condyle is almost perfectly flat, but it has a larger transverse than antero-posterior diameter. In these animals all the mechanical arrangements of the joint are subsidiary to the grinding movements of the back teeth; hence the flatness of the condyle, which is separated from the flat glenoid cavity by a thin, flat meniscus. The capsule of the joint is very lax, and, as might be expected, there is a much larger joint surface between the glenoid cavity and the meniscus than between the latter and the condyle. There is no *eminentia articularis*, but the post-glenoid process is always present. The pig differs from the ruminants in that the post-glenoid process is only present at the inner part of the back of the joint. The glenoid cavity is more concave from before back, and the condyle is more transversely elongated and convex antero-posteriorly. In the horse the glenoid cavity is concave from side to side, and convexo-concave from before back, as in man. The meniscus is concavo-convex antero-posteriorly above and rather deeply concave below, while the post-glenoid process is well marked. In many ways the temporo-maxillary joint of the horse is much more like that of the Primates than that of the Ruminants, such as the ox, deer, and sheep.

In the Sirenia, the order comprising the dugongs and manatees, I have never had a chance of dissecting the joint, but in the dried skull the glenoid cavity is flat, and of very moderate extent. The condyle is transversely elongated, and somewhat convex from before back. It does not at all correspond with the shape of the glenoid cavity, and it is reasonable to expect that the meniscus is well developed.

In the Rodentia, the temporo-maxillary articulation is quite characteristic; perhaps the capybara, agouti, or viscacha show the joint surfaces in their best development. The glenoid

cavity is an antero-posterior gutter instead of a transverse one as in the Carnivora; it is deeply concave from side to side, and the top slopes somewhat downward and forward. There is absolutely no pre- or post-glenoid process to check the condyle in its forward or backward movement. The condyle in the dried skull seems to fit this groove very imperfectly. Its long axis

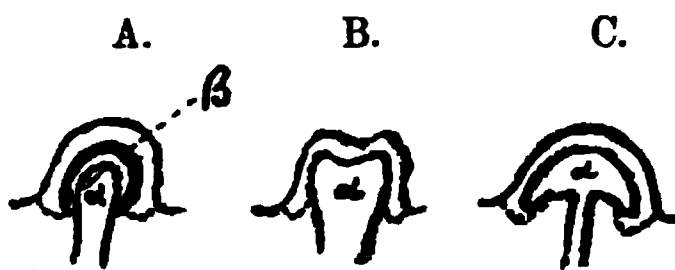


FIG. 3.—Coronal sections through the temporo-maxillary joints of A. A, rodent; B, armadillo; C, *Ornithorhynchus*. a, condyle; β, meniscus.

is antero-posterior, and it is convex from side to side. When it is placed in the glenoid cavity there is a considerable gap on each side of it. This is filled up by the meniscus, which is closely attached to the condyle, but quite loosely to the skull, so as to allow free antero-posterior gliding movement. The anterior and posterior parts of the capsule, although allowing free play for this movement, are quite strong enough to check it when it has gone far enough. The rabbit is a singularly bad example of a rodent as far as its jaw joint goes. In it the glenoid cavity is extremely shortened from before back, and the forward and backward play of the condyle is much less than in the more typical animals. The jerboa is another rodent in which the forward and backward play of the mandible is poorly marked. In both of these animals the incisors are not very strong, and probably have not the same part to play as in the beaver, squirrel, or agouti.

The Edentata, as far as their temporo-maxillary joint is concerned, may be divided into the anteaters and the toothed forms. In the pangolin (*Manis*), which is an anteater, and only opens its mouth wide enough to allow its slender tongue to be protruded, there can hardly be said to be any condyle or ascending ramus to the mandible, but there is a meniscus which is closely attached to the jaw, and which allows free lateral and considerable antero-posterior movement between itself and the glenoid cavity.

In the armadillo (*Dasypus*), the glenoid cavity resembles that of the rodents in forming an antero-posterior groove (see fig. 3, B.), but in the roof of this groove an antero-posterior ridge is present which fits into a depression on the top of the condyle.<sup>1</sup> It is remarkable that in the three specimens of armadillo which I have had the chance of examining the meniscus was absent in every case.

The Marsupialia present the most varied forms of temporo-maxillary articulation. The kangaroos, in the first place, have an almost typical ruminant glenoid cavity and condyle, the chief difference between the glenoid cavity of the kangaroo and the sheep being that that of the former is in proportion longer antero-posteriorly than is that of the latter.

This is one instance of many of the adaptability of joints to the habits of their possessors, an adaptability much more marked than is the case with muscles. The phalangers have an articulation intermediate between the ruminant and carnivorous types, the condyle is elongated from side to side, and convex from before back, while the glenoid cavity is concave in its posterior part, but anteriorly is prolonged as a flat gliding surface. This type of jaw is adapted to the food of the phalanger, which consists of leaves and birds. The bandicoot's and opossum's jaws closely agree with the last, and the meniscus is slight. The wombat (*Phascolomys*) has teeth like a rodent's, but its jaw does not at all resemble the rodent type; it does, however, somewhat remind one of the same structure in the rabbit. The condyle is very much elongated transversely, but is short and convex from before backward; it is also somewhat convex from side to side. It articulates with a glenoid cavity, which is an antero-posteriorly compressed bar, also convex from before backward, but somewhat concave from side to side. It must require a well marked biconcave meniscus and very strong ligaments to adapt these two dissimilar joint surfaces to one another, but I have not had an opportunity of dissecting the soft parts of this animal.

The carnivorous Tasmanian devil (*Dasyurus ursinus*) has a typical carnivorous jaw articulation resembling that of the fox

<sup>1</sup> I saw this ridge in two specimens of *Dasypus villosus*, but it was not present in one of *D. sexcinctus*.

or dog, in the absence of a pre-glenoid process. In the specimen which I dissected there was no trace of a meniscus.

In the Monotremata, the *Echidna*'s jaw resembles that of the pangolin in the absence of any definite condyle, but the meniscus is absent. In the *Ornithorhynchus* the condyle is markedly convex from side to side, and somewhat convex from before back. The two halves of the jaw are not united at the symphysis, and the chief movement which the animal seems to perform is a rotation round an antero-posterior axis passing through the neck of each condyle; the result of this is that the margins and the more central parts of the horny bill are alternately pressed together by the masseter and pterygoid muscles, and the animal is enabled to bruise and press the water weeds on which it lives.

It was not to be hoped that the study of the temporo-maxillary articulation in the Mammalia would give much information about the morphological significance of the inter-articular fibro-cartilage, and the only facts which my dissections have taught me are that the meniscus is a very constant structure in the Mammalia, but that it may be suppressed or undeveloped in certain animals. The four animals in which I have noted its absence are *Dasypus*, *Dasyurus*, *Ornithorhynchus*, and *Echidna*. The two former I suspect are cases in which the structure has been suppressed, because they are the only genera in their respective orders in which absence of the meniscus has been noticed, but in the case of the Monotremata there is no sign of any meniscus in either animal; and although it may be objected that *Echidna* is an animal whose jaws are very rudimentary, it will be found that they are not so rudimentary as those of *Manis*, in whom a distinct meniscus is present. Besides considering the question whether the temporo-maxillary meniscus is the homologue of the quadrate or quadrato-jugal, or any other reptilian structure, it is necessary to think whether it may not be a new development adapted to the requirements of the higher mammals, and formed from the tissues surrounding the joint, in the same way that the semilunar cartilages of the knee and other interarticular structures are. The small amount of evidence which I have been able to extract from the Mammalia seems to favour this view, because if the meniscus represents

some reptilian structure, the Monotremata are the animals in which we should expect to find some transition, whereas these are just the animals in which no trace of a meniscus is found.

#### THE ARTICULATIONS OF THE CLAVICLE.

The presence of the clavicle, as is well known, is very variable, and when it is present it is so feebly developed in some cases as not to reach the sternum on the one hand or the scapula on the other. All the Primates have well developed clavicles, which differ very little in their articulations from those of man. Perhaps the chief point which strikes one in examining the sterno-clavicular articulation of the lower Primates is the fact that the sternal articular facet is much more dorsal than in man, and its direction is, taking the animal as being in the upright position, upward, outward, and backward. Keith describes the meniscus as being replaced in the cynomorphous monkeys by a fibrous ligament, which allows the two articular cavities to communicate. In the three specimens of *Macacus* and one each of *Cynocephalus sphinx* and *Cercopithecus lalandii* which I have examined, the meniscus in all respects resembled that of man.

In the spider monkey (*Ateles paniscus*), I only found one articular surface, and that was chiefly between the clavicle and first rib. In the lemur the interarticular cartilage is well developed and the synovial cavities as in man.

In the lower Primates it is only possible to make out one coraco-clavicular ligament, but whether this represents the conoid, trapezoid, or both, I do not know. In the acromio-clavicular articulation of *Macacus* the acromial surface is slightly though distinctly convex from side to side, while the clavicular surface is flat, the capsule dips in from above and forms a very slight attempt at an intra-articular fibro-cartilage. In *Ateles* and *Lemur* no trace of this is present. Among the *Cheiroptera*, *Pteropus* and *Plecotus* have little movement at the sterno-clavicular joint. The joint surface is almost horizontal and the clavicle runs upward and slightly outward from it. The chief movement is one of rotation of the long axis of the clavicle, combined with slight elevation and depression. There is no inter-articular fibro-cartilage or intra-clavicular ligament



but the rhomboid ligament is very strong. In the acromio-clavicular articulation there is no sign of any intra-articular structure.

All the Insectivora except one have well developed clavicles, but my own knowledge of their joints rests on a dissection of the mole, the hedgehog, and the shrew. At the sternal end of the clavicle of the hedgehog there is a short rod of cartilage

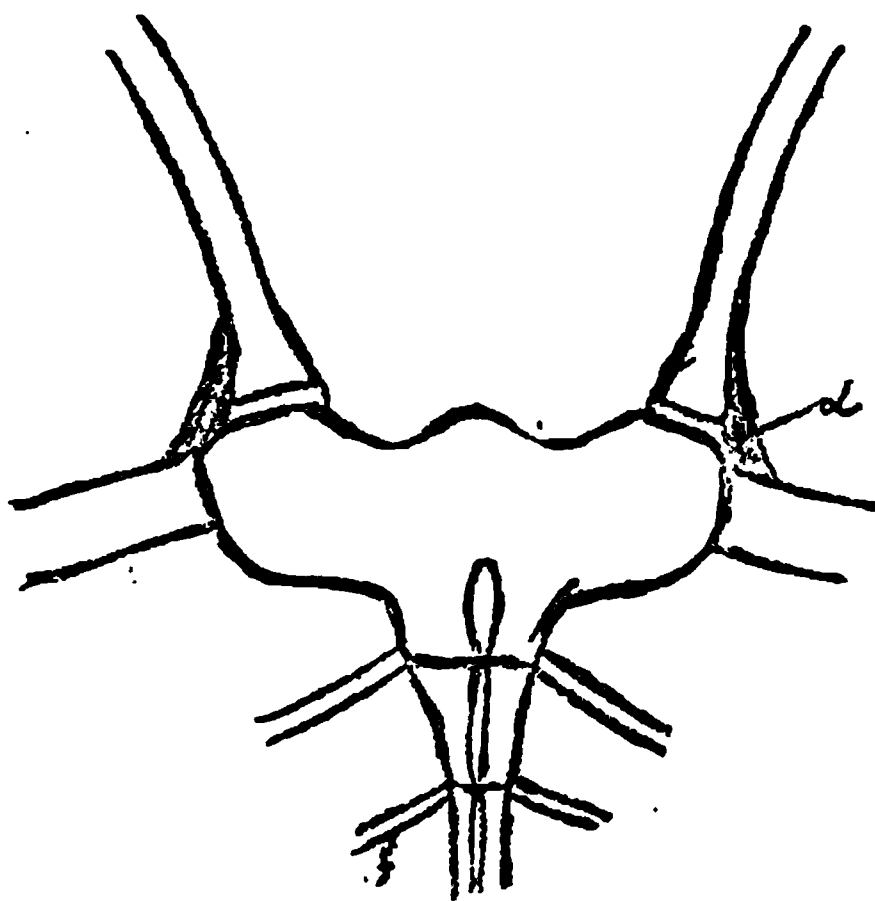


FIG. 4.—Sterno-clavicular articulations of Fruit Bat (*Pteropus*).  
a, rhomboid ligament.

which articulates with the antero-dorsal part of the sternum by a synovial cavity. The capsule which keeps the two joint surfaces together is lax, but the ventral portion of it is especially strong.

In the mole, there is a long antero-posterior (ventro-dorsal) surface on the sternum with which the clavicle articulates. There is no meniscus, and the upper (cephalic) portion of the capsule is very strong. A well marked acromio-clavicular ligament connects these two parts, but the distal end of the short clavicle articulates with a large facet on the great tuberosity of the humerus.

In the shrew, the arrangement is practically identical with that of the hedgehog.

The articulations of the Carnivora, Cetacea, Sirenia, and

Ungulata need not detain us, since in these animals the clavicle, even if it is present, is a mere spicule of bone.

In the Rodentia, the clavicle is generally cartilaginous at both ends, and in the cartilaginous rod between the bony clavicle and the sternum an ossific nodule occurs in adult animals. I have examined several rats and voles of different ages, but have been unable to discover any extra ossific nodule which would correspond to the sternal epiphysis of the clavicle of the Primates. In many genera, such as the squirrels, lemming, jerboas, and the Cape jumping hare (*Pedetes*), the clavicle is very well developed, and is attached to the side of the manubrium by fibro-cartilage, in which sometimes a joint cavity is found. The acromio-clavicular joint I have never seen in Rodents; the clavicle has always been connected with the acromion by cartilage or fibrous tissue. The coraco-clavicular ligament is present when the clavicle is at all well developed, and is attached to the dorsal border of the clavicle.

In the Edentata, the Aardvark (*Orycteropus*) and the armadillo have well developed clavicles; in the latter the sternal end articulates with the dorsal surface of the manubrium by a short rod of cartilage without synovial cavities.

The acromion is very long, and articulates with the clavicle by a synovial joint. At the acromial extremity of the clavicle there is a very long coraco-clavicular ligament. The rudimentary clavicle of the three-toed sloth, as Lydekker has pointed out, is attached to the coracoid instead of the acromion process, and this arrangement is doubtless an enlarged coraco-clavicular ligament, akin to that of the armadillo, combined with a suppression of the acromio-clavicular communications. It is interesting to notice that the two-toed sloth (*Choloepus*) has a perfectly normal clavicle connected with the acromion.

Among the Marsupialia, the bandicoot (*Perameles*) is the only form in which the clavicle is not developed. In the Tasmanian devil (*Dasyurus*) the sternal end is cartilaginous, and is connected with the sternum by fibrous tissue, as in many rodents. This is also the case in the pigmy flying phalanger (*Acrobates pygmea*), but in the vulpine phalanger there is a distinct joint cavity between this cartilage and the sternum at one end, and the clavicle at the other. At the acromial end of the clavicle

is a joint cavity without any intra-articular structures. In the Monotremata the clavicle is firmly fixed on to the inter-clavicle, but there is a joint cavity between it and the acromion process, which is unprovided with any intra-articular structure, and allows only slight gliding movement.

With regard to the morphology of the inter-articular meniscus, the general opinion is that it represents the so-called omosternal or suprasternal ossifications, which Gadow looks upon as the remains of the ventral ends of one or more cervical ribs. It is perfectly true that in animals such as the shrew and the Monotremes, the omosternum, suprasternum, or inter-clavicle, which, I believe, are identical structures, occupy the position which the inter-articular menisci do in the Primates, and it seems almost querulous not to be satisfied with an explanation which has so much in its favour; still, it must be borne in mind that inter-articular cartilages, as such, only occur in the Primates, and if Keith is right, only in the higher Primates. It may be that all inter-articular menisci are formed in some mechanical manner, of which we know nothing at present, from the structures surrounding the joint. As I go on, I shall try to show that a combination of rotation with gliding or hinge movements often is coincident with the formation of menisci, and I would specially call attention to the knee of the fruit bat and the fibulo-astragalar joint of many marsupials as cases in point. One must not attempt to dogmatise from the study of mammals alone, but I think that the possibility of all menisci having a similar physiological origin from extra-capsular structures is worth bearing in mind.

### THE SHOULDER.

In the human shoulder joint it is usual to teach that the lax capsule is reinforced by the coraco-humeral ligament, and it is suggested that this represents the continuation of the tendon of the pectoralis minor.<sup>1</sup> Three gleno-humeral folds are also

<sup>1</sup> Rosenfeld, in a paper on the Ligaments of the Shoulder Joint in Man and Mammals (*Anat. Hefte*, xi., 1898, p. 341), agrees with a good many of my observations, though in some points we differ materially. The time at my disposal only allows me to refer to his paper.

described in the front of the joint, though their exact attachments vary in different accounts. According to Quain's description, the upper one runs horizontally in front of the tendon of the biceps, which, encased in synovial membrane, lies free in the joint cavity. The second comes from the top of the glenoid cavity with the last, but runs obliquely downward and outward to the inner side of the small tuberosity. The inferior runs from the notch in the middle of the anterior border of the

2

FIG. 5.—Shoulder joint of Man, opened from behind. From *Quain's Anatomy*.

glenoid cavity to the lower part of the neck of the humerus. The highest of these is supposed to represent the ligamentum teres of the hip joint by some.

In dissecting the shoulder joint of catarrhine monkeys (*Macacus*, *Cercopithecus*, and *Cynocephalus*), I noticed that although the pectoralis minor passed over the coracoid process and was inserted into the capsule of the shoulder, a fairly well marked coraco-humeral ligament was also present, and quite distinct from it. From this I am led to believe that the coraco-humeral ligament of man may be reinforced by the distal

fibres of the pectoralis minor, but that it is not entirely representative of them. It seems quite logical to assume that in animals in which the fore-limbs have been converted from organs of support into those of occasional traction, the connective tissues above the joint would become thickened and strengthened quite independently of any muscle.

I have never yet seen any animal, except man, in which the tendon of the biceps is free in the shoulder joint; it is always connected to the capsule by a reflection of synovial membrane from its anterior margin. Again, as Bland Sutton points out, one, and only one, gleno-humeral ligament is seen; he figures it in the beaver with accuracy, and gives a list of rodents in which it is equally well developed. I have also observed the ligament in a large number of rodents, and can bear testimony to the truth of his assertions as far as these animals go, but in the list of other mammals, in which he declares that the ligament "was as well developed as represented on p. 58,"<sup>1</sup> I can only agree with him to a slight extent. As discrepancies

FIG. 8.—Shoulder of Macaque Monkey, opened from behind.  
a, biceps tendon; B, bursa under subcapularis; c, gleno-humeral ligament.

in the description of anatomical structures may occur without either observer being necessarily in error, I shall content myself with describing my own observations, and will leave future investigations to decide those points on which we differ. In the Primates, I examined three macaques—a vervet, a colob, and a baboon—as examples of the old world monkeys. In all of

<sup>1</sup> *On the Nature of Ligaments.*

these, as Keith points out,<sup>1</sup> the biceps was not free in the joint cavity, and the gleno-humeral ligament was represented by a delicate fold of synovial membrane, which ran downward and outward from the top of the glenoid cavity where the biceps arose, and was lost in the lower part of the capsule. This fold was below the pouch of synovial membrane which projects from the front of the joint between it and the subscapularis tendon, and, I have no doubt, corresponds to the middle gleno-humeral ligament of the human anatomy text-books. Bland Sutton states that in the gorilla, orang, and chimpanzee the gleno-humeral ligament is absent, but I am able to show a specimen of the orang's shoulder, from the museum of this College, in which the ligament is very fairly developed. In no member of

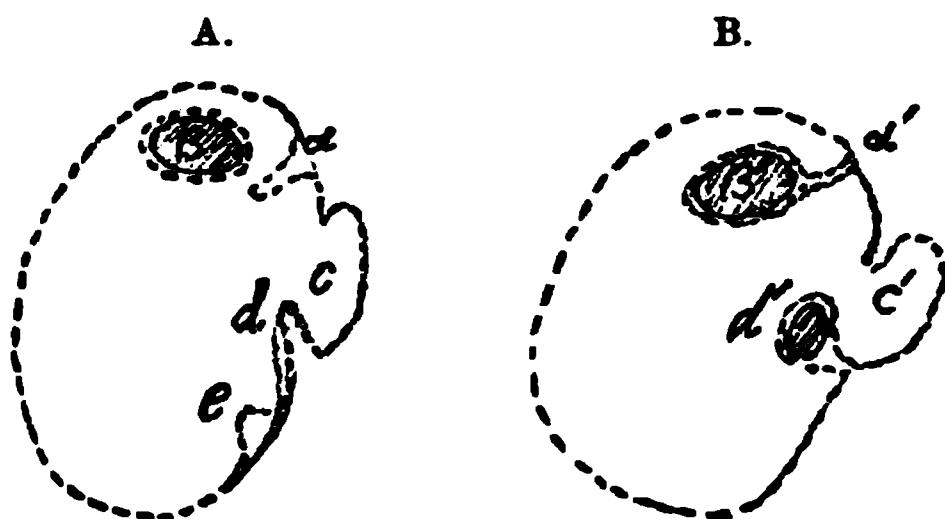


FIG. 7.—Diagrammatic sections through shoulder joint of A, Man ; B, typical Mammal. *a*, superior gleno-humeral ligament; *a'*, reflections of synovial membrane on to biceps; *β β'*, section of biceps; *c c'*, pouch under subscapularis; *d d'*, middle gleno-humeral ligament; *e*, inferior gleno-humeral ligament.

the Primates but man, nor indeed in any other mammal, is there a superior gleno-humeral ligament; and when one remembers that in man alone the biceps tendon is free in the joint, one is forced to the conclusion that the superior gleno-humeral ligament of man is the remains of the mesentery-like reflection of synovial membrane which in all other mammals is attached to the front (ventral border) of the biceps. It has been said that this superior gleno-humeral ligament of man is the representative of the ligamentum teres in the hip. To my mind the explanation I have just proposed is more reasonable; and it seems a remarkable thing that in man alone of the Mammalia the

<sup>1</sup> *Journ. of Anat.*, vol. xxviii. p. 163.

serial homologue of the ligamentum teres should be present. In the spider monkey (*Ateles paniscus*) the gleno-humeral fold is less developed than in the Catarrhini, and only forms the valvular free lower edge of the pouch under the subscapularis. In the lemur the gleno-humeral ligament is about as well developed as in the macaque monkey, but it does not form the lower limit of the pouch of synovial membrane, which lies not only deep to, but also over the top of, the subscapularis tendon.

In the fruit and insectivorous bats (*Pteropus* and *Plecotus*) among the Cheiroptera, the biceps tendon is entirely outside the capsule of the joint. The gleno-humeral ligament is moderately distinct, and runs from the top of the joint to the lower part of the lesser tuberosity. In the Insectivora, the hedgehog shows a

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FIG. 8.—Shoulder of Hedgehog (*Erinaceus*), opened from behind.  
a, biceps tendon; b, pouch under subscapularis; c, gleno-humeral ligament.

fairly well marked gleno-humeral ligament with the usual attachments, but instead of being a mere infolding of the synovial membrane, as in the animals hitherto described, it stretches across the mouth of the subscapularis pouch, and thus in its upper part is free in the joint. In the mole, I was unable to detect any gleno-humeral ligament at all. In the Carnivora, there may or may not be a gleno-humeral ligament; when it is present it is feebly developed, and is only marked in the upper part of its extent. I found it in the hyena, dog, ichneumon, and otter, but failed to find any trace in the black bear.

In the Ungulata, the ligament was fairly well marked in the deer and antelope (*Cariacus* and *Tragelaphus*), it was attached

to the upper margin of the glenoid cavity dorsal to the origin of the biceps, passed across the mouth of the opening into the subscapularis pouch, and below faded away into the capsule. In the goat it was less well developed, and in the chevrotain (*Tragulus*) absent altogether. In *Hyrax* there was a very large opening into the subscapularis pouch, the lower margin of which is horizontal, prominent, and fringed. I do not, however, think that it represents a gleno-humeral ligament. In the elephant the ligament is absent.

Of the shoulder joint of the Sirenia and Cetacea, I have no knowledge.

In the Rodentia, the gleno-humeral ligament reaches its maximum development; it is perhaps seen at its best in members of the hystricomorphine sub-order. Looked at in such animals as the viscacha, capybara, or agouti, it will be seen as a broad, strap-like ligament attached above to the margin of the glenoid cavity on the dorsal side of the origin of the biceps, and below to the lower part of the lesser tuberosity of the humerus. The ligament is contained in a sheath of synovial membrane, and is free in the cavity of the joint, except in the lower part of its course, where it passes between the capsule and the synovial membrane. In the jerboas and Cape jumping hare, the structure is not nearly so well developed as in other rodents. That this ligament is the same as the middle band of man is proved by its having the same attachments and relation to the subscapularis pouch. Among the Edentata, the armadillo has a strong gleno-humeral ligament, but the pangolin and tamandua have none. In the armadillo which I dissected, the dorso-cephalic part of the capsule was thickened to form a distinct ligament; it is well known that in this animal the transverse humeral ligament is ossified to form a bony canal for the biceps.

In the Marsupialia, the kangaroo shows a fringed fold corresponding in position to the part of the gleno-humeral ligament nearest the glenoid cavity. In the *Dasyure* the structure is fairly definite, and in the bandicoot, pigmy phalanger (*Acrobates*), and vulpine phalanger very definite. In the Monotremata, the shoulder differs considerably from that of other mammals. In *Ornithorhynchus*, the glenoid cavity is deeply concave ventro-dorsally, convex from side to side; it may be described as a deep



furrow forming a segment of a circle, and having a longer dorsal or scapular lip, and a shorter ventral or coracoid one. The head of the humerus is exactly adapted to this; it is convex ventro-dorsally and crescentic, the hollow of the crescent fitting against the ventral (coracoid) lip of the glenoid cavity. As the crescent glides round this pivot, the humerus is rotated on its long axis, and the forearm, which is at an acute angle with it, moves forward and back in the plane of the long axis of the body. Flexion and extension of the shoulder are very slight, and so are adduction and abduction; when the hand requires to be brought away from the side, the chief movement occurs between coracoid and sternum. A strong ligament passes from the coracoid lip of the glenoid cavity to the hollow or ventral side of the crescent-shaped head of the humerus. These are the attachments of the gleno-humeral ligament throughout the Mammalia; and I have little doubt that this ligament in *Ornithorhynchus* is not only a gleno-humeral ligament in name, but the homologue of the ligament which bears the same name in other mammals.

There is another ligament outside the shoulder capsule of *Ornithorhynchus* which runs from the base of the coracoid to the humerus, but I hesitate to claim for it any homology with the coraco-humeral ligament in man, because between the Monotremata and the Primates there is a gap in which the coraco-humeral ligament is ill-developed or wanting, and also because the greater part of the coraco-humeral ligament of man comes from the epicoracoid rather than the coracoid element. The shoulder joint of *Echidna* corresponds very closely with that of *Ornithorhynchus*.

### THE ELBOW JOINT.

The elbow joint of monkeys differs little from that of man in the arrangement of the bony surfaces. In the capsule there is often a strong oblique band lying superficial to the general mass of capsular fibres, and passing from the internal condyle downward and outward to just above the tubercle of the radius; it becomes tightly wound up in extreme pronation, and checks that movement. I found this band in the spider and vervet monkeys, not in the macaque or baboon.

The internal lateral ligament of the rhesus monkey differs from that of man in only consisting of one very strong band which runs downward and backward to the shaft of the ulna some distance below the margin of the coronoid process, the brachialis anticus being inserted between it and the bone. There is no band between the condyle and the olecranon as in man. The external lateral ligament also runs downward and backward from the front of the outer side of the external condyle; its most superficial fibres pass down to the shaft of the ulna, the deeper ones blend with the orbicular ligament. It will thus be seen that both these ligaments tend to check extension of the elbow, a function of great importance when one

FIG. 9. — Elbow of Spider Monkey (*Ateles*), from in front. *a*, oblique epitrochleo-radial ligament; *b*, anterior ligament of capsule; *c*, orbicular ligament.

considers the length of the monkey's forearm and the greater leverage which it exerts. This arrangement of ligaments applies also to the spider and vervet monkeys and to the baboon, but in the lemur the three fasciculi of the internal lateral ligament are present as in man, though the external lateral ligament is continued down to the shaft of the ulna as in the monkeys. In all the Primates the orbicular ligament is very strong, and on cutting it and pulling apart the bones of the forearm a feeble quadrate ligament may be seen.

In the Cheiroptera, the fruit bat (*Pteropus*) has an elbow in

which pronation and supination of the radius are only possible for about one-eighth of a circle. The ulna is very feeble, and only articulates with the back of the articular surface on the humerus, consequently the trochlear surface is only present posteriorly. The upper part of the olecranon is separate, and attached to the rest by fibrous tissue. The whole of the front of the humeral articular surface is in contact with the large and transversely elongated head of the radius, and both the external and internal lateral ligaments are attached to the sides of this. The internal lateral ligament runs down some distance on the neck of the radius, and the biceps is inserted between it and the bone. The external lateral ligament has a sesamoid bone developed in it which plays on the outer side of the head of the radius. There is no orbicular ligament. The radius is in a position of semi-pronation, so that the pollex is nearer the head than the other digits.

In the Insectivora, the hedgehog has the kind of elbow which is typical of those mammals which use their fore-limb for support. The radius is strongly pronated and its head is oval, with the

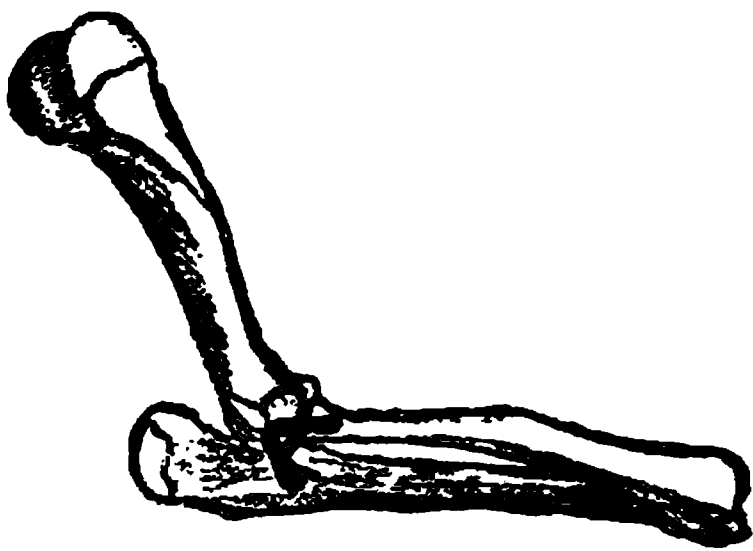


FIG. 10.—Elbow of Hedgehog (*Erinaceus*), from the inner side.

long axis directed transversely; it forms the anterior or horizontal part of the great sigmoid cavity, the ulna forming the vertical or posterior portion. The lesser sigmoid cavity looks directly forward, and the head of the radius lies altogether in front of the ulna. There is no orbicular ligament, and the external lateral ligament is feeble. There are two well marked fasciculi of the internal lateral ligament from the internal condyle, the anterior passing to the radius, the posterior to the ulna. When

the joint is flexed a very large amount of lateral movement is allowed, but when it is extended this is checked.

In the mole, the elbow is specialised for digging; the head of the radius lies by the side of the ulna, and there is a bony projection running up from it behind the capitellum of the humerus, just as the olecranon runs up behind the trochlea. This projection is bound to the olecranon by a strong ligament. The lateral ligaments of the joint are well marked, but there is no orbicular ligament, and practically neither pronation nor supination is allowed.

In the Carnivora, there is considerably more pronation and supination, often to the extent of a quarter of a circle; and to adapt the joint to this, an orbicular ligament is present, which in

FIG. 11.—Elbow of *Ichneumon* (*Herpestes*), from the outer side.

the bear is extremely thick. The familiar instances of a kitten playing with a ball of worsted or a bear climbing a pole will remind everyone that considerable pronation and supination are possible to these animals.

The external lateral ligament is attached to the orbicular, and is then prolonged some distance down on the neck of the radius. In the hyæna I found it twisted so that the fibres which were anterior above became external and eventually posterior. The oblique ligament (epitrochleo-radial) already referred to in

monkeys is present in *Procyon*, *Herpestes*, and *Mustela*, but not in *Ursus* or *Hyæna*; it has the same attachments and checks pronation. Also coming from the internal condyle, there are anterior and posterior internal lateral ligaments, though one or other of these is occasionally wanting.

The ungulates have an elbow adapted entirely for support; the head of the radius supports the whole weight of the fore part of the body, the olecranon merely forming a projection behind to prevent forward dislocation. The external and internal lateral ligaments are strong, and are both attached to the radius below. There is no pronation, and therefore no orbicular liga-

FIG. 12.—Elbow of Raccoon (*Procyon*), from the inner side. *a*, oblique epitrochleo-radial ligament; *β*, internal lateral ligament.

ment, but the radius and ulna are bound together by external and internal superior radio-ulnar and strong interosseous ligaments, which in the adult horse and ox tend to ossify. In *Hyrax* the elbow is less typically one of support, the ulna is much more by the side of the radius, while the internal lateral ligament, which is double, passes to the ulna instead of to the radius; there is, however, no orbicular ligament.

In most of the *Rodentia* the arrangement very closely resembles that of *Hyrax*; the radius is in front and to the outer side of the ulna, and its head is elongated transversely, so that pronation to the extent of about one-sixth of a circle is all that is possible, and there is no orbicular ligament. The lateral

ligaments closely resemble those of Hyrax. It is interesting to notice that certain rodents which do not use their fore-limbs for support, such as *Pedetes* and *Dipus*, have the head of the radius circular and capable of pronation to the extent of quarter of a circle, and that in them an orbicular ligament is present. What I have seen of mammalian elbows makes me believe that when pronation to the extent of quarter of a circle or more is possible, an orbicular ligament is always present.

Among the Edentata, *Bradypus* and *Manis* have definite orbicular ligaments, although the amount of pronation is slight; the external lateral ligament is attached to it as well as to the neck of the radius, while the internal lateral passes to the ulna. In *Dasypus*, on the other hand, the radius has a transversely elongated head and no orbicular ligament, so that pronation is impossible. This animal is remarkable for the laxity of the capsule of the elbow, and the amount of lateral movement allowed during flexion of the joint.

In the Marsupialia, the elbow joint varies a good deal, especially in the amount of pronation of the radius. In the Kangaroos (*Macropus* and *Petrogale*) pronation to the extent of nearly quarter of a circle is allowed, and there is a well marked orbicular ligament. In the bandicoot (*Perameles*) the joint closely resembles that of man, the radius has a circular disc-shaped head, rotating in a well marked orbicular ligament for about three-eighths of a circle, and the ligaments are arranged much after the human fashion. In the Opossum (*Didelphys*), on the other hand, although pronation to the extent of nearly quarter of a circle is possible, I quite failed to detect any orbicular ligament.

In the Monotremata, the elbow joint of the *Ornithorhynchus* is a perfect hinge. The articular surface on the humerus looks downward and forward, and is convex from above down as well as from side to side; its long axis is transverse. The posterior part of the sigmoid cavity is formed by the ulna, the lower by the radius. There is no orbicular ligament, and no pronation or supination is allowed. The radius and ulna are connected by interosseous ligament, and a certain amount of gliding can take place. In the *Echidna* the same arrangement exists, but prona-

tion and supination to the extent of less than one-eighth of a circle is possible.

From the foregoing it will be seen that there are two main types of elbow: firstly, that of the monotreme or ungulate, in which the head of the radius is transversely elongated, situated more or less immovably in front of the ulna, and having both lateral ligaments attached to it. Secondly, that of the Primates, in which the head of the radius is a circular disc rotating in an orbicular ligament by the side of the ulna, and in which the lateral ligaments pass either directly or indirectly to the ulna. The first of these is best adapted for support, the second for prehension, and towards one or other of these the various elbows of mammals tend.

#### WRIST JOINT.

In the human wrist one notices, among other things, that the styloid process of the ulna is very small and does not articulate with any of the carpal bones, that the pisiform

FIG. 13.—Wrist of Macaque Monkey, from palmar side. *a*, radio-carpal ligament; *β*, ulno-carpal; *S*, scaphoid bone; *M*, os magnum; *P*, pisiform; *C*, cuneiform; *U*, unciform; *ES*, radial ossicle in external lateral ligament.

does not take any part in the formation of the wrist joint, that it articulates with the cuneiform by a synovial cavity,

which is quite separate from all others, and that there is no attempt, at least in the adult, at division of the joint into outer and inner parts by an antero-posterior septum. On comparing this human joint with that of a rhesus monkey, the much greater comparative size of the styloid process of the ulna is at once apparent, and this styloid process, during adduction of the hand, fits into a cup-shaped socket formed by the cuneiform and pisiform bones; moreover, the articulation between the cuneiform and pisiform bones communicates with the cavity of the wrist. The fibres of the anterior ligament of the wrist run in two directions. The radio-carpal fibres run downward and inward, while the ulno-carpal are on a more superficial plane, and run downward and outward from the styloid process of the ulna to the scaphoid.

In man, it will be noticed that, with the diminution of the styloid process, the ulno-carpal ligament has disappeared. In the vervet (*Cercopithecus lalandii*), the arrangement is practically identical with that of the rhesus, except that there is a slight projection of synovial membrane into the front of the joint, corresponding to the junction between the radius and the triangular fibro-cartilage above, and to that between the semilunar and cuneiform bones below. In the baboon (*Cynocephalus sphinx*), this partial septum is more distinct, but in all these three monkeys the triangular fibro-cartilage closely resembles that of man. In the spider monkey (*Ateles paniscus*), the joint between the radius above and the scaphoid and semilunar below is completely cut off from that between the ulna and cuneiform by an antero-posterior septum. The styloid process of the ulna is large and hemispherical at its lower extremity; it fits into a concave facet on the upper surface of the cuneiform, but the pisiform does not form any part of this facet. The arrangement of the triangular fibro-cartilage of this animal is interesting; there is no sigmoid cavity on the lower end of the radius, but the fibro-cartilage, which is really a wedge-shaped mass of fibrous tissue, is attached to the lower half inch of that bone, and against this fibrous tissue the articular surface of the ulna plays. At its highest point the fibro-cartilage is continuous with the interosseous membrane, and the arrangement in this and several other mammals are suggestive of the



possibility that, after all, the triangular fibro-cartilage of the wrist may be nothing more than the separated lower end of the interosseous membrane. I should, however, state that the hypothesis which seems to find most favour at present is that the triangular fibro-cartilage is an ingrowth from both the palmar and dorsal parts of the capsule, and that it possibly contains in it the rudiments of an extra ulnar digit.

In the lemur the wrist joint closely resembles that of *Ateles*; the styloid process of the ulna is still more enlarged, so that it

FIG. 14.—Inferior radio-ulnar joint of Spider Monkey (*Ateles*).

is a distinct continuance of the shaft, instead of a small excrescence as in man, and its hemispherical articular surface is received into the usual cup formed by the cuneiform and pisiform bones.

From the radial attachment of the fibro-cartilage a septum completely divides the wrist joint into a radial and ulnar half. It is interesting to notice that Prof. Leboncq has already found that in an early stage of the development of the wrist of the human foetus the triangular cartilage is attached, not only to the radius and ulna, but to the semilunar as well. In the Chiroptera, the wrist is so modified for the purpose of flight that most of our landmarks have disappeared. In the first place, the ulna in the fruit bat (*Pteropus*) disappears in the lower part of the forearm, and the cuneiform, having no forearm bone to articulate with, is greatly reduced in size. The pisiform has entirely disappeared, and the scaphoid and semilunar are fused to form a large scapho-lunar, the upper articular surface of which is shaved off in front and behind, so as to form a transversely elongated wedge, which fits into a trough exactly adapted to it.

on the lower end of the radius. The two bones are held together by palmar, dorsal, and lateral ligaments, and it is evident that here is a joint which will allow a small amount of hinge movement, and that only; a joint which it would be extremely difficult to dislocate.

In the Insectivora, the hedgehog has the radius and the ulna closely bound together inferiorly; and as there is no synovial cavity between the lower ends of these bones, the ligament representing or occupying the same place as the fibro-cartilage of the Primates is continuous with the interosseous membrane. The ulna is, as usual, received into a facet formed by the cuneiform and pisiform.

In the Carnivora, the scaphoid and semilunar are always fused, and the joint between the scapho-lunar and radius is often partially, and may be completely, shut off from that between the ulna, cuneiform, and pisiform. When the partition is incomplete it is, as usual, situated in the anterior (palmar) part of the joint. The ulno-carpal ligament from the lower end of the ulna to the palmar surface of the scapho-lunar is usually very well marked. It has already been pointed out that carnivores allow a good deal of pronation and supination of the forearm, and in connection with this a synovial cavity between the lower ends of the radius and ulna, and above the triangular fibro-cartilage seems always present.

In the Hyæna, this fibro-cartilage consists of two distinct parts: an inferior, in which the fibres are antero-posterior, and are continued into the palmar and dorsal ligaments of the joint; and a superior, in which they pass transversely from the radius to the ulna. This direction of the upper fibres is suggestive of their being a separated part of the interosseous membrane.

In the Ungulata, the wrist is more exclusively a hinge than in the Insectivora or Carnivora, where a certain amount of abduction and adduction is allowed. The radius alone forms the upper joint surface in the greater number of animals, and articulates with the scaphoid, semilunar, and cuneiform by several ridges and furrows. In the brocket deer (*Cariacus*) I found, on opening the joint from the dorsum, a vertical fold of synovial membrane projecting from the palmar ligament, and partially cutting off the joint between the radius and cuneiform

from that between the radius, scaphoid, and semilunar; this, however, I failed to notice in other ungulates. In the harnessed antelope (*Tragelaphus scriptus*) two external lateral ligaments were seen: the superficial one ran to the side of the great metatarsal bone, while the deep passed between the radius and scaphoid; this latter was distinctly twisted in such a way that the fibres which above were on the radial side became anterior (dorsal) lower down, and finally on the ulnar side. Both these ligaments become tight on extension.

In Hyrax, the wrist is more generalised than in the true ungulates; both ulna and radius enter into it, and the cavity between the ulna and cuneiform is completely cut off from the rest of the wrist, as in so many mammals. Both the radius and ulna have a dorso-ventral ridge which fits into a corresponding depression in the carpal bones of the first row, and must check lateral movement.

In the Rodentia, as a rule, the joint is not divided into radial and ulnar portions by a partition, but the lower end of the ulna is peg-shaped, and fits into a cup formed by the cuneiform and pisiform. In the part of the joint between the radius and scapho-lunar, the bony surfaces are irregularly convex and concave.

In Bradypus and Dasypus, among the Edentata, the wrist is not divided into two, but in Manis the part between the ulna and cuneiform is completely shut off. In Dasypus the ulno-carpal ligament is especially strong, and runs as usual from the ulna to the scaphoid.

Among the Marsupialia, Macropus, Petrogale, Didelphys, and Phalangista have the joint completely divided into radial and ulnar halves. In Dasyurus the peg-like lower end of the ulna is as usual received into the cup formed by the cuneiform and pisiform, but there was apparently no division of the joint.

In the Monotremata, both Ornithorhynchus and Echidna have the ulna entering rather more largely into the formation of the wrist than the radius, and the partition between the radial and ulnar halves of the joint is attached to the margin of the ulna above and to the scapho-lunar below; this is somewhat different from the usual arrangement, and it is worthy of notice that in the Mammalia generally the lower attachment of this partition to

the inner (ulnar) edge of the semilunar is much more constant than its upper attachment, which may be to the ulnar edge of the radius (most mammals), to the middle of the lower surface of the radius (*Cariacus*), or to the radial edge of the ulna (*Monotremata*). In the *Monotremata* there is an antero-posterior notch on the scapho-lunar, into which a corresponding ridge on the radius fits, and prevents any rotation or lateral movement.

Summing up, we find that the generalised mammalian wrist is nearly a perfect hinge, and that it is divided into two lateral parts, that the ulna fits into a cavity formed by the cuneiform and pisiform, that the triangular fibro-cartilage, as such, can hardly be said to exist, and that it is represented by an interosseous ligament, which appears to be a thickened part of the interosseous membrane, and that the palmar portion of the capsule consists of a superficial ulno-carpal and a deep radio-carpal ligament, which together form an X. The effect of a moderate amount of supination seems to be, as in the carnivores, to form a synovial cavity above the triangular fibro-cartilage and to emphasise that structure, also to interfere with the dorsal part of the septum, dividing the wrist into two lateral parts. More perfect supination, as in man, leads to a greatly increased inferior radio-ulnar joint, and to complete disappearance of the vertical partition of the wrist (though this is present in the foetus). The necessity for extensive adduction is correlated with diminution of the lower end of the ulna into the little styloid process, and total exclusion of the pisiform from the wrist. With the reduction of the lower end of the ulna, the ulno-carpal ligament disappears.

AN EXPERIMENTAL CONTRIBUTION TO THE STUDY  
OF THE MECHANISM OF BILE SECRETION. By  
WILLIAM BAIN, M.D. Durham, M.R.C.P. Lond.

(From the Physiological Laboratory of St Thomas's Hospital.)

THE following facts regarding the influence of the nervous system upon the secretion of bile have been gleaned from the literature of the subject.

1. Heidenhain (1) found that section of the splanchnic nerves which causes a dilatation of the radicles of the portal vein increases the flow of bile.

2. Munk (2) observed that stimulation of the splanchnic nerves, by producing a constriction of the arteries and a consequent slowing of the portal stream, retards the biliary secretion.

3. Section of the spinal cord in the neck diminishes the flow, owing to the fall of pressure throughout the vascular system.

4. It has been assumed that the biliary secretion is not directly controlled by the nervous system, because experiment has shown that pilocarpine (3), while increasing the flow of saliva and the pancreatic juice, has no effect on the flow of bile; and atropine (4), which inhibits other secretions, fails to arrest the biliary.

5. Stimulation of the spinal cord, whether induced directly or reflexly, leads to a diminution in the flow. It is known that stimulation of the vagus nerves does not affect the secretion when the animal is under an anæsthetic. To eliminate the factor of anæsthesia, I decided to use the methods adopted by Pawlow in proving that the vagus was the secretory nerve to the stomach and pancreas, viz.—a dog was pithed, tracheotomy rapidly performed, and artificial respiration established. A cannula was then inserted into the common bile duct, the cystic duct clamped, and the vagus nerves exposed in the neck. The cannula was attached by rubber tubing to a glass capillary tube about 3 feet 6 inches in length, having a capacity of 1

cubic centimetre, and graduated into 100 divisions, each division being subdivided into halves, so that readings could easily be taken and timed. Coloured water was used as an index. The capillary tube was retained in a horizontal position.

### EXPERIMENT I.

A dog weighing 16 lbs. was placed under ether. The operative procedures just described were performed, and the vagus nerves stimulated alternately by gradually increasing currents from an induction coil.

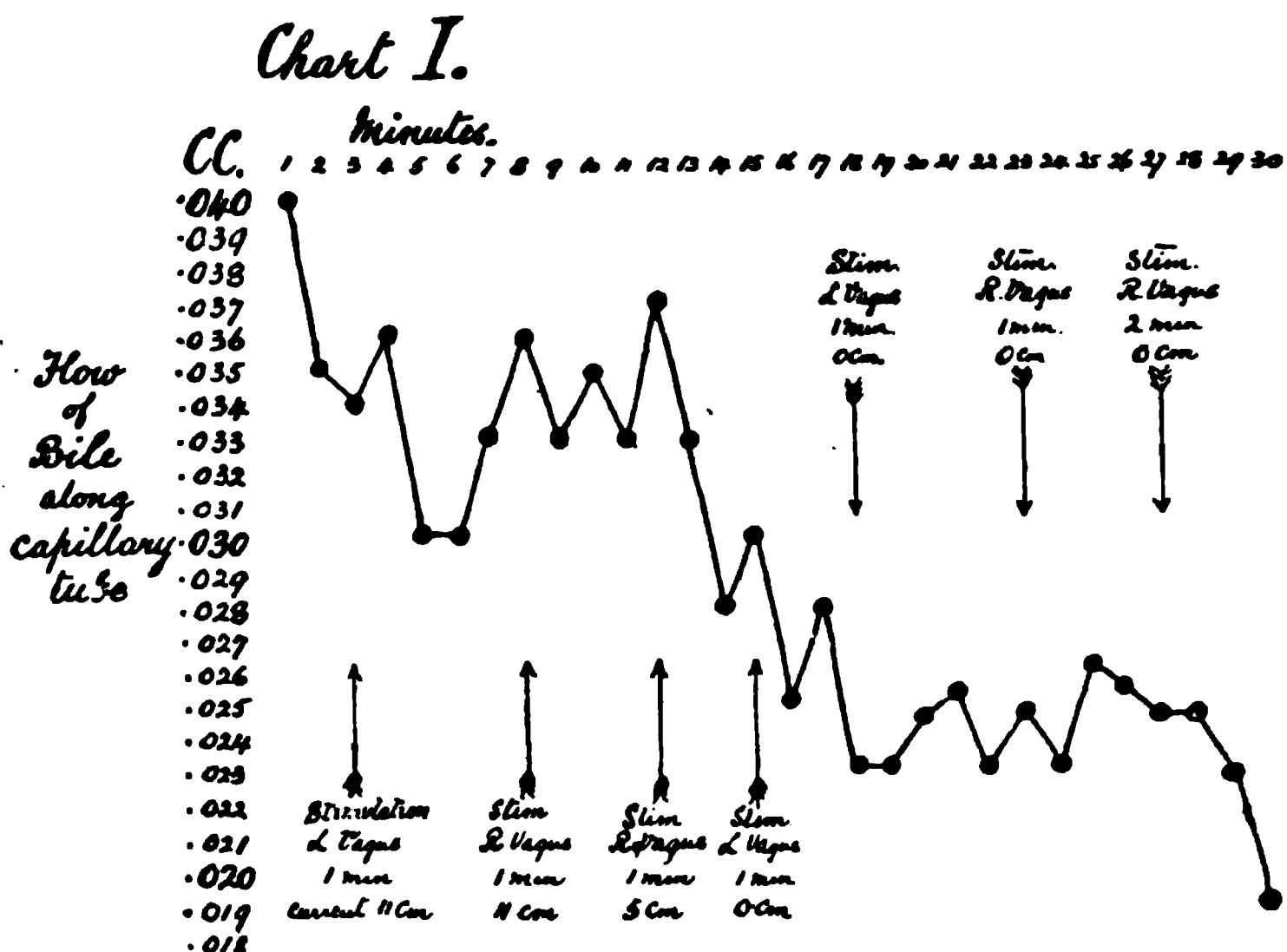


Chart I. clearly demonstrates that stimulation of either vagus has no influence on the secretion of bile.

The charts are constructed on the basis of the rate of secretion per minute. This is obtained by dividing the number of divisions over which the index travels by the number of minutes the index takes to traverse these divisions.

In comparing Chart I. with Chart II. it will be observed that although the rate of secretion is somewhat diminished by section of the spinal cord in the neck, it is not markedly so, as is generally stated.

## EXPERIMENT II.

A dog weighing 17 lbs. was put under ether. The usual operation for connecting the bile duct with the recording capillary tube was performed.

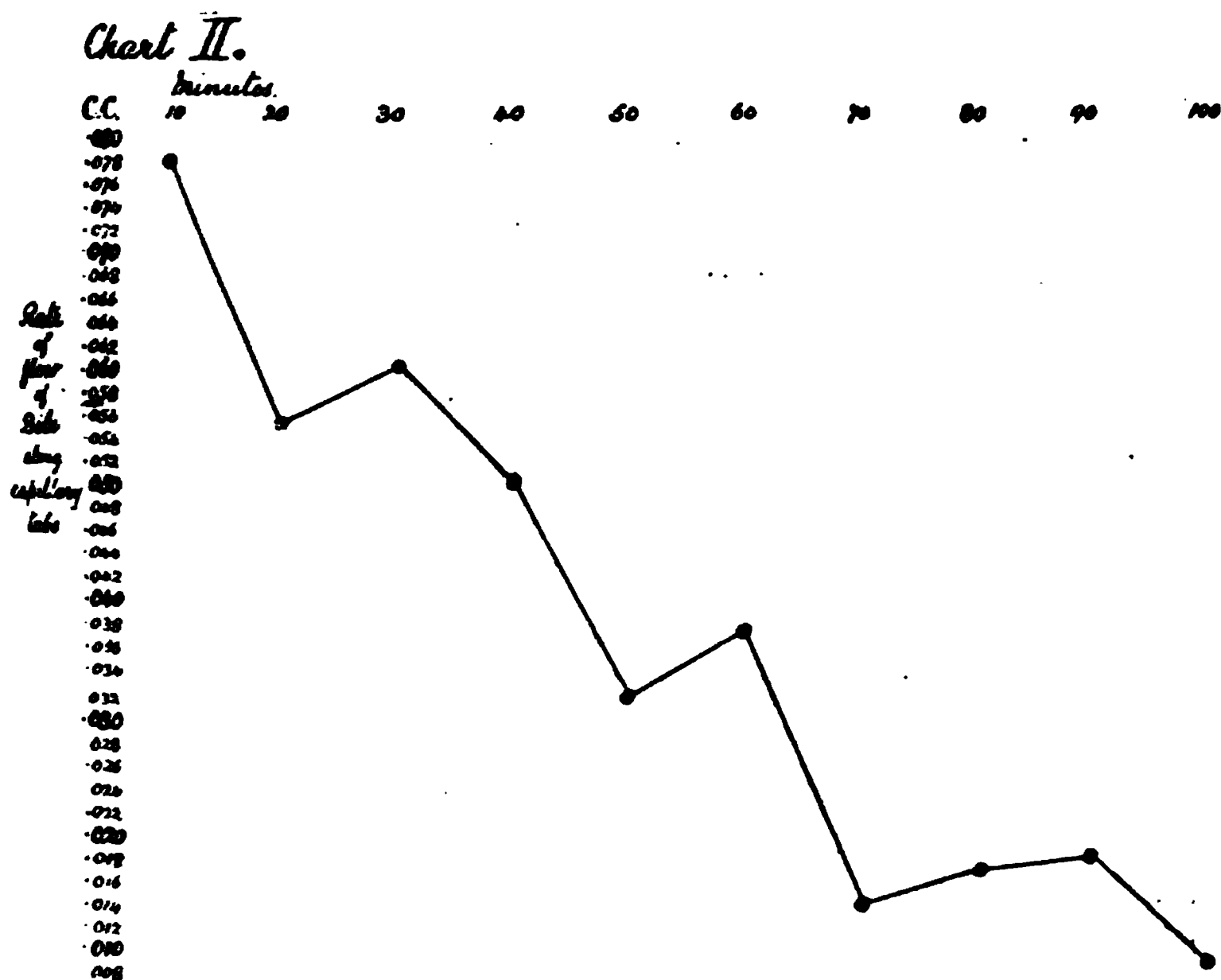


Chart II. shows the gradual fall that normally occurs in the rate of secretion as the bile drains away from the system.

The manner in which cholagogues act on the liver is still a matter of surmise. Rutherford (6) has pointed out the difficulty of ascertaining the factors which determine an increase of bile after the administration of a particular drug. He says the increase may be occasioned "(1) by stimulation of the hepatic secreting apparatus; or (2) by stimulation of the muscular fibres of the gall bladder and larger bile ducts, to wit, the bile-expelling apparatus; or (3) by removing a catarrhal or congested state of the orifice of the common bile duct, or of the general extent of the larger bile ducts; or (4) by removing from the intestines substances which had been passing therefrom into

the portal vein and depressing the action of the hepatic or (5) by stimulating the intestinal glands, and thus promoting drainage of the portal system, whereby the loaded liver possibly be relieved."

Doubtless some drugs act by stimulating the muscular of the bile ducts and the intestinal mucosa, while others may both on the bile ducts and the liver cells. I tried to ascertain if the secretion of bile would be affected by injecting of drugs in solution directly into the circulation. If a drug injected into the external jugular vein increased the secretion of bile, the deduction, I think, would be that it stimulated secretory cells of the liver.

### EXPERIMENT III.

A dog weighing 33 lbs. was put under ether. The cannula tube having been connected with the common bile duct in the usual way, a cannula was inserted into the external jugular vein and the vein clamped below the insertion of the cannula. In every case save repetition, it may be stated that the subsequent experiments were carried out in a similar manner. Fifty c.c. of 0.9 per cent. chloride of sodium solution was injected into the vein, the dose being repeated after an interval of one hour. Afterwards a solution of Plattner's crystals was injected, and repeated at a further interval. (See Chart III.)

Chart III. shows a slight but unsustained increase after the first saline injection, and a distinct increase after the second injection, of Plattner's crystals. Probably the first injection of Plattner's crystals was too small to have an effect.

It is evident from this experiment that the injection into the circulation of 100 c.c. saline solution has little if any effect in accelerating the flow of bile, whereas a comparatively small dose of Plattner's crystals has a distinct effect.

### EXPERIMENT IV.

A dog weighing 14 lbs. was injected with 15 c.c., and after an interval 50 c.c. of strong sulphur water (Harrogate) at a temperature of 37° C. All the solutions were injected at the





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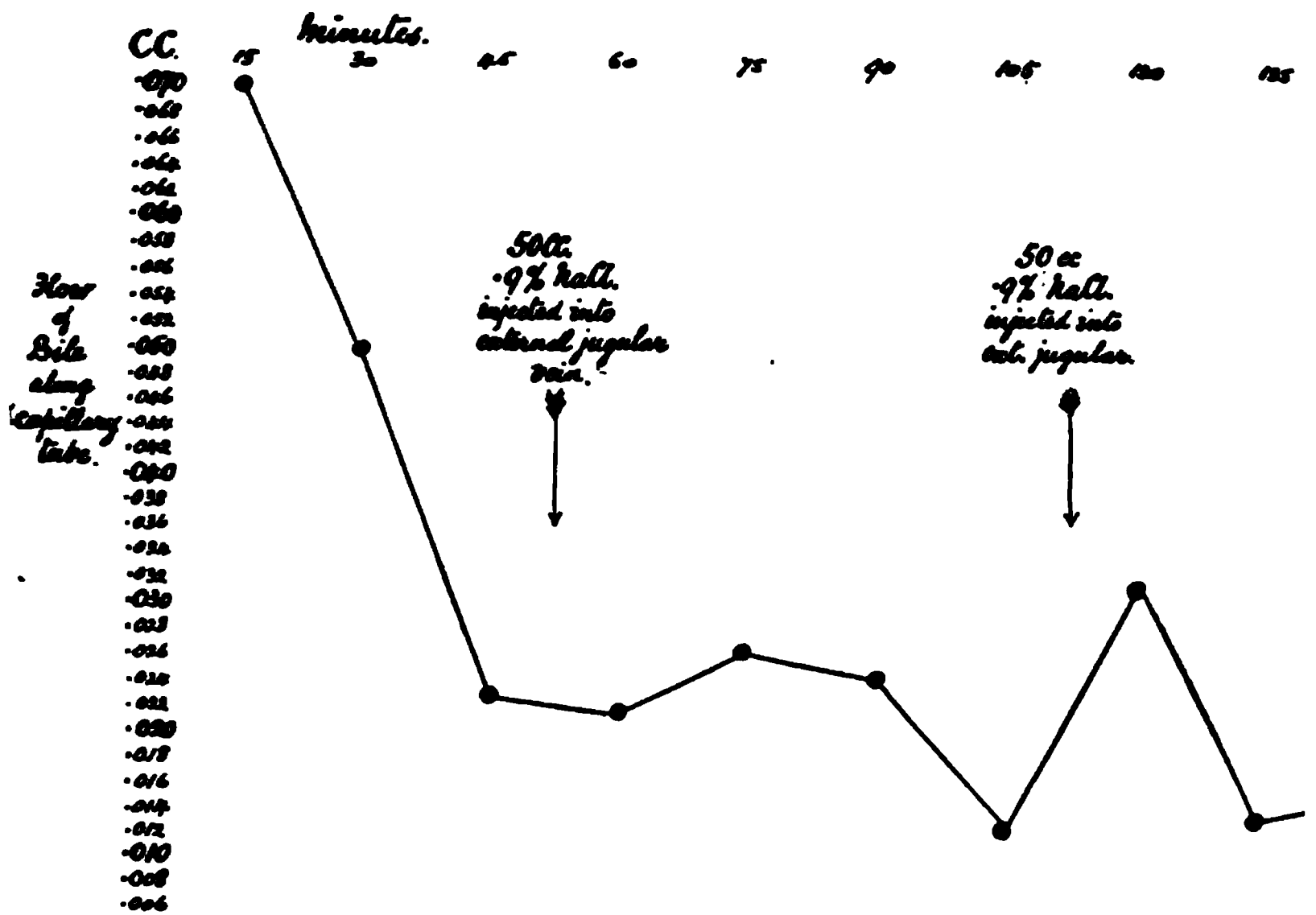
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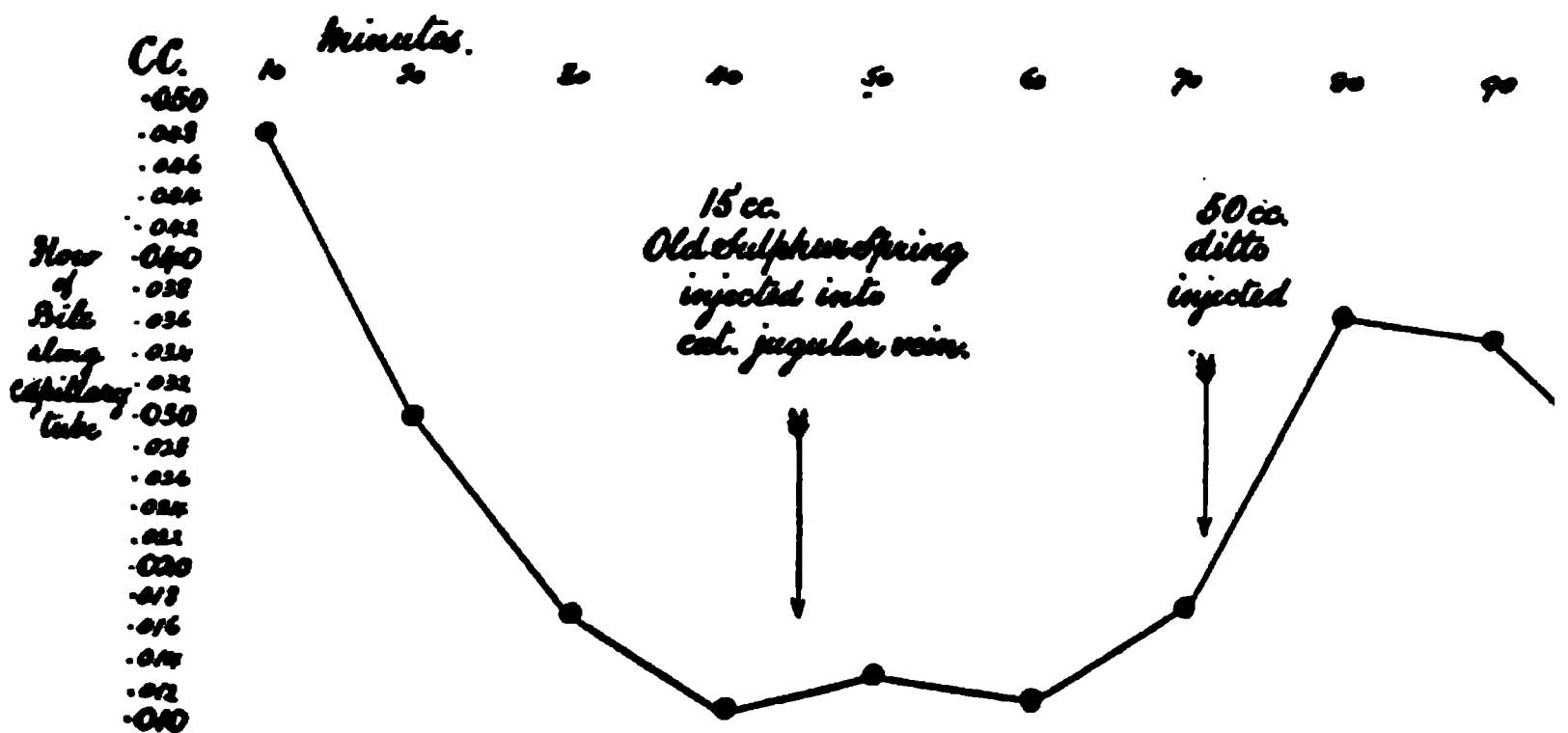
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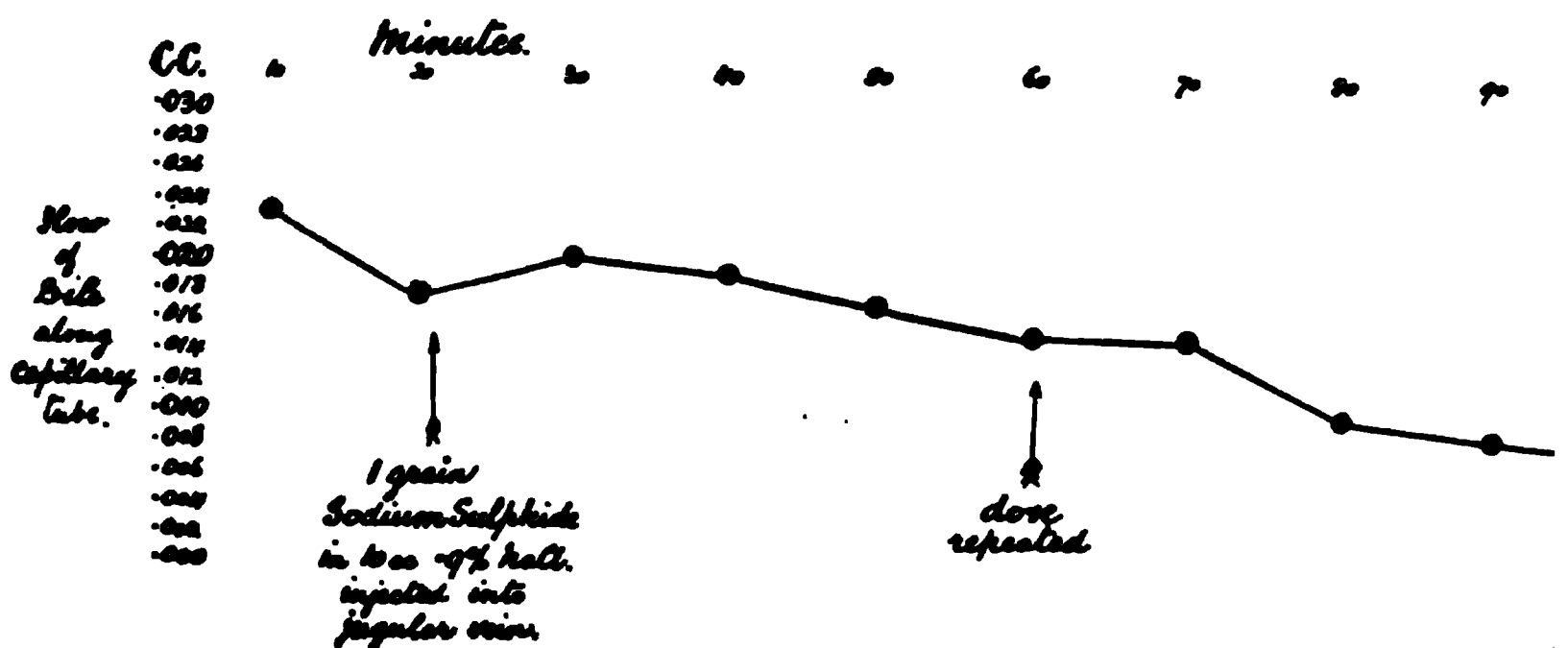
### Chart III.



### Chart IV.



### Chart VI.





same temperature. This substance was selected because in a previous investigation it was found to increase the flow of bile considerably. (See Chart IV.)

Chart IV. shows after the second injection a distinct and sustained increase in the rate of flow. In this case also probably the first dose was too small to produce an effect.

From this experiment, one is clearly justified in assuming that the sulphur water stimulates the secretory cells of the liver.

The next point I endeavoured to determine was the particular ingredient in the sulphur water which produced the increase in the rate of secretion. Sulphide of soda, magnesium chloride, and barium chloride were tried. The results are inconclusive.

#### EXPERIMENT V.

A dog weighing 15 lbs. was injected with 3 grains of sulphide of soda in 20 c.c. of a 0.9 per cent. saline solution, and after an interval a similar dose was given.

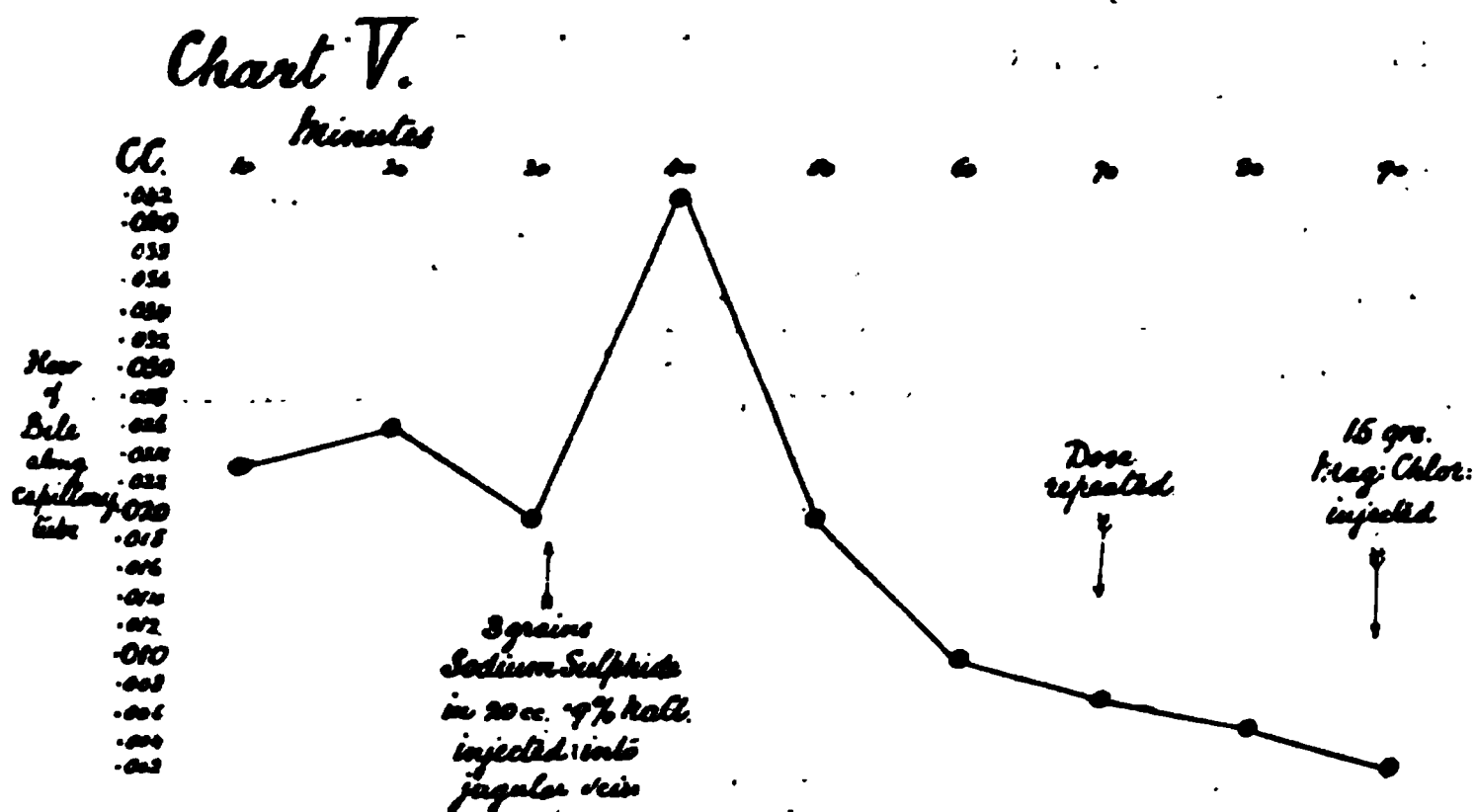


Chart V. shows a distinct rise after the first injection of the soda salt, but on repeating the dose no effect was observable. On injecting 15 grains of magnesium chloride the dog immediately died.

## EXPERIMENT VI.

A dog weighing 18 lbs. was injected with 1 grain of sodium sulphide in 10 c.c. of saline solution. There was only a slight increase in the rate of flow, but the fall which normally occurs was delayed. On repeating the dose scarcely any effect was noticed. Two injections of small doses of magnesium chloride had no effect. Then three-quarters of a grain of barium chloride was used. The rise was marked, but the dog succumbed fifteen minutes after. (See Chart VI.—previous page.)

Chart VI. shows the result of two injections of sodium sulphide, two of magnesium chloride, and one of barium chloride.

I have pleasure in expressing my indebtedness to Dr Brodie for his valuable assistance during the experiments.

The conclusions to be drawn from these experiments appear to be:—

1. That stimulation of either vagus has no influence on the secretion of bile.
2. That 100 c.c. of saline solution directly injected into the circulation has little or no effect on the flow of bile.
3. That Plattner's crystals and the Old Sulphur Well (Harrogate) stimulate the secretory cells of the liver.
4. That the ingredients to which the sulphur water owes its efficacy as a cholagogue are probably barium chloride and sulphide of sodium.

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  - (3) PASCHKIS, *Med. Jahrb.*, Wien, 1884, s. 169.
  - (4) RUTHERFORD, *Action of Drugs on the Secretion of Bile*, Edinburgh, 1880.
  - (5) LICHTHEIM, *Inaug. Diss.* Berl., 1867.
  - (6) RUTHERFORD, *loc. cit.*
  - (7) BAIN, *Journal of Anatomy and Physiology*, 1898, vol. xxxiii. p. 91.

NOTE ON A GROUP OF VARIETIES OF THE PECTORAL  
SHEET OF MUSCLE.<sup>1</sup> By THOMAS H. BRYCE, M.A.,  
M.B., F.R.S.E.

THE group of anomalous muscles which is the text of this note was found in a female subject aged 62. The left pectoral sheet was normally disposed, but on the right side the superficial manubrial portion of the pectoralis major was in great part absent, and there were present sternalis, sterno-clavicularis, and chondro-epitrochlearis muscles. The occurrence of such a series

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of varieties of the same pectoral sheet is uncommon, and I have thought the case worthy of being recorded, partly on this account, but also because its features are of theoretical interest in relation to the morphology of the sternalis and the sterno-clavicularis.

<sup>1</sup> Read before the meeting of the Anatomical Society of Great Britain and Ireland, 26th April 1899.

The sterno-clavicularis arose from the side of the manubrium sterni, and by tendinous fibres from the second costal cartilage. The outer part of this tendinous origin was not attached to the cartilage, but directly continuous with the upper tendon of the sternalis, presently to be described. The muscle was attached above to the clavicle along its antero-inferior border, mainly by fleshy fibres, but at the outer end by a tendinous portion, which extended to the outer third of the bone under the deltoid. The greater part of the muscle lay beneath the clavicular head of the pectoralis major, on the costo-coracoid membrane, but at its inner end it came to the surface, owing to the defect in the great pectoral. The superficial manubrial section of that muscle was represented only by a narrow band, which crossed the surface of the sterno-clavicularis to join the upper border of the muscular mass arising from the body of the sternum. Between this manubrial band and the clavicular head there was a distinct interspace, but between it and the gladiolar section a considerable triangular interval was left, in which, as it were, the normal superficial fibres were displaced by the deeper abnormal layer. The sternalis had a short muscular belly, 2 in. long by  $\frac{3}{4}$  in. broad, between two tendons. The lower tendon was attached to the aponeurosis of the external oblique, on a level with the seventh costal cartilage, the upper was in part attached to the second costal cartilage, but at its outer side was continued directly into the outer part of the tendinous origin of the sterno-clavicularis, as described above.

The chondro-epitrochlearis arose from the outer end of the sixth costal cartilage, and was closely applied to the deep surface of the pectoralis major. On reaching the arm it passed downwards under the deep fascia to the inner side of the biceps, to be inserted into the internal intermuscular septum, 2 inches above the internal epicondyle. It was a band  $\frac{3}{4}$  in. broad, and remained fleshy to its insertion; usually the muscular fibres end on a rounded tendon, on a level with the insertion of the pectoralis major.

The nerve supply of the sternalis was not definitely ascertained, as the parts had been disturbed before my attention had been drawn to the muscle, but the sterno-clavicularis received,



on its deep aspect, a branch of some size from the external anterior thoracic nerve.

In his "Catalogue of Muscular Varieties"<sup>1</sup> Professor Macalister describes two muscles arising from the first costal cartilage and manubrium, and inserted into the clavicle—1st, Supraclavicularis; 2nd, Præclavicularis medialis. He notes a case in which he found the first associated with a rectus sternalis, a levator claviculæ, a chondro-epitrochlearis, and an achselbogen,—much the same group of varieties as in the present case.

Testut<sup>2</sup> does not distinguish the two varieties, but describes them both under one head, as sterno-clavicularis anterior, arising from the sternum below the sternal head of the sterno-mastoid, and inserted into the inner, middle, or outer third of the clavicle. The muscle may, however, arise from the first rib cartilage, the anterior sterno-clavicular ligament, or the sternal tendon of the sterno-mastoid (supraclavicularis of Macalister), or from the lower part of the manubrium (Wood), and in my case it extends to the second costal cartilage. It is covered by the pectoralis major, and separated from the subclavius by the costo-coracoid membrane.

The muscle evidently represents a portion of the deep lamella of the pectoral sheet arising from the manubrium, and it is significant that when present, either in its single or its double form (interclavicularis anterior digastricus), there is frequently a defect in the pectoralis major. In my case it is the manubrial portion that is defective, and it looks as if the deeper muscle, not usually present, had displaced the fibres normally springing from the lower part of the manubrium and the second costal cartilage. It is, however, as a rule—corresponding to the more usual origin of the sterno-clavicular fibres from the upper part of the manubrium or first costal cartilage—the inner part of the clavicular head, sometimes including the upper part of the manubrial portion, that is wanting, and in this case the defect may be looked upon as having the same explanation.<sup>3</sup>

<sup>1</sup> *Trans. Roy. Irish Acad.*, vol. xxv.

<sup>2</sup> *Les Anomalies Musculaires chez l'Homme*, etc., 1884.

<sup>3</sup> See a case described by Dwight, *Jour. Anat. and Phys.*, vol. xxii., 1888, p. 98.

The sterno-clavicularis is therefore, in virtue of its position, a "deep manubrial slip,"<sup>1</sup> and, in virtue of its innervation, belongs to the same category as the pectoralis minimus, and the other slips described as arising from the same point. They may all be regarded as different forms of the part of the deep lamella of the pectoral sheet, usually suppressed in man, arising from the manubrium, and supplied by the external anterior thoracic nerve.

So much has been written on the sternalis, and such general interest taken in it, that I need make no comment on the general question, except to point out the bearing of the case on Professor Cunningham's theory as to the nature of the muscle. He writes:<sup>2</sup> "the appearance of the parts produced the impression that the sternalis had been formed by a deviation or dislocation of the pectoral fibres from above, downwards and inwards. The nerve of supply (external or internal anterior thoracic) is dragged inwards by the deviating fibres, and this accounts for its great length. . . . But additional proof . . . is found in the occasional recurrent course of the intercostal nerves. This suggests in the most striking manner the probability that the nerves have been pushed inwards by the deviating fibres." Again referring to the cases in which a sternalis is associated with a defect in the pectoralis major (in anencephalic foetuses), he says:<sup>3</sup> "it is reasonable to suppose that the gap is caused by the abstraction of this portion of the muscle to form the sternalis."

The case under consideration, so far as it goes, tends distinctly to support this theory as to the nature of this much described muscle; and applying it to the individual case, it seems reasonable to conclude that the sterno-clavicularis, coming to the surface on the manubrium and second costal cartilage, has caused a displacement of the superficial fibres arising normally from these parts, and that these fibres have been dislocated downwards and inwards to form the sternalis, in the manner suggested by Professor Cunningham.

<sup>1</sup> For Windle's subdivision of the pectoral sheet according to its innervation, see his paper in *Trans. Roy. Irish. Acad.*, vol. xxix.

<sup>2</sup> *Jour. Anat. and Phys.*, vol. xxii., 1888, p. 399.

<sup>3</sup> *Loc. cit.*, p. 400.

## UPON THE PRESENCE OF ADRENAL STRUCTURES IN THE INGUINAL CANAL. By C. B. LOCKWOOD.

IN my Hunterian Lectures on "The Development and Transition of the Testis,"<sup>1</sup> I described lipomata of the spermatic cord, and the specimens were placed in the museum of St Bartholomew's Hospital.<sup>2</sup> Similar growths have been described by Curling, Stonham, and Hutchinson junior. Whilst discussing the production of these lipomata, I said that in foetuses it is quite usual to find that a quantity of sub-peritoneal fat accompanies the processus vaginalis into the scrotum. I inferred, therefore, that lipomata of the spermatic cord originated in portions of the sub-peritoneal fat which had accompanied the transition of the processus vaginalis. At this time lipomata of the cord did not seem to possess much practical importance, but during the past ten years operations for the cure of inguinal hernia have become the commonest operations that surgeons are called upon to perform. Moreover, I have in cases of doubt frequently explored the inguinal canal. During these operations small fatty tumours have often been met with attached to or surrounding the hernial sac. In the exploratory operations, the inguinal canal has frequently been found to contain a mass of fat, instead of a hernial sac such as was expected to be found. When we consider that these fatty tumours are mistaken for ruptures, and the patient condemned to the lifelong wearing of a truss, their practical importance becomes obvious. Whilst operating for the radical cure of hernia in a little boy, a congenital hernial sac was met with in the left inguinal canal, but in addition a small fatty tumour was likewise present. The latter was excised along with the sac, and sent as usual to the pathological department for histological examination. As a result, my colleague, Dr F. W. Andrewes, has made sections, which clearly show that the bodies, which had the appearance of lobules of fat, were in reality a number of small adrenal

<sup>1</sup> *Journal of Anatomy and Physiology*, vol. xxii., 1888.

<sup>2</sup> Specimen 2812a.

bodies. Mr A. Norman has made from these sections some very clear micro-photographs, which are here reproduced. Fig. 1 gives a general idea under a low power,  $\times 25$ . The growth is surrounded by a loose fibrous capsule, in which a few blood-vessels run. Here and there, upon the outer surface of this capsule, a little adipose tissue is seen, whilst from the inner surface fibrous septa divide the small adrenal bodies from one another. Under a higher power,  $\times 65$ , the bulk of these miniature adrenal bodies consist of a vast number of cells, arranged in groups which in section are wedge-shaped. The base of the wedge

FIG. 1.

is in contact with the fibrous capsule, whilst the apex converges along with all the others towards the centre (fig. 2). Near the centre is a small lumen which receives a number of lymph spaces, which radiate out from it towards the periphery and intervene betwixt the various columns of cells. The columns of cells are likewise separated by a small quantity of very delicate connective tissue, which is continuous with the inner surface of the fibrous capsule, and makes a frame-work for the support of the cells. The latter consist of a nucleus, which is the size of a white blood corpuscle, and in addition a little globule of fat enclosed in the cell membrane. The position of the nucleus with regard to the fat varies considerably. Not infrequently

it is situated at the periphery of the cell, and being slightly flattened, produces the well known signet-ring cell. A glance at the accompanying figures shows that we have here to deal with a structure with the very closest resemblance to the adrenal bodies. Although the point is not shown in the figure, because a higher magnification is required (Zeiss D, eyepiece 3), the fibrous capsule has within its substance a number of small loculi of cells, which are nucleated and laden with fat, but so arranged as to simulate very closely the appearance of a scirrhous cancer.

In volume xxii. of the *Journal of Anatomy and Physiology*,<sup>1</sup> I described and figured a specimen which throws light upon the origin of these adrenal bodies. This specimen was

FIG. 2.

obtained from a human embryo, which had reached somewhere about the seventh week of intra-uterine life. A very complete and perfect series of longitudinal sections was obtained from this embryo. An electrotpe was made from a micro-photograph of one of these sections. I am indebted to my friend Mr Cosens for the trouble which he took in making

<sup>1</sup> Page 472, fig. 47.

these. Towards the right of the section is seen the developing kidney, with its glomeruli and tubules, and below the kidney towards the left a considerable length of ureter can be seen. Along the front of the kidney is the lower end of the suprarenal body, which at this stage of development is of enormous size, larger than the kidney itself. (See also fig. 47, *Hunterian Lectures*, on the Development and Transition of the Testis, by C. B. Lockwood.) But the lower end of the suprarenal body can be distinctly followed to where its lower end lies in front of the ureter and far below the kidney. This lower part of the suprarenal body has a very striking appearance, because it contains numbers of glomeruli. The lowest of these glomeruli are exceedingly distinct, but the upper ones become more difficult to see, and are gradually lost in that part of the suprarenal body which lies in front of the kidney. Other sections of the series show that that which appears to be a glomerular portion of the suprarenal body is, as a matter of fact, the upper part of the Wolffian body. Other sections show that the lower part of the Wolffian body is connected with the genital mass, and is in process of conversion into the epididymis, or into the parovarium. Without waiting to discuss the light which this series of sections throws upon the development of the adrenals from the upper part of the Wolffian body, I would remark that it clearly proves that in a human embryo the adrenals reach much lower than is generally thought. In fact, they occupy not only the hilum of the kidney, but also extend along the course of the ureter as far as the ovary or testicle. The ureter is mentioned because it can be so clearly seen in the section; but it would, perhaps, be more correct to say that it extends along the course of the spermatic or ovarian vessels.

A similar continuity of adrenal body and epididymis was also seen in an older embryo, but in this case the large size of the renal veins made it more difficult to see. It is hardly necessary to point out what direct relation this observation has to the presence of adrenal structures in the inguinal canal. I am not aware that the significance of these retro-peritoneal remains of the Wolffian body has been pointed out. The frequency with which Wolffian remains in the neighbourhood of the ovary gives origin to cysts would suggest that cysts might

be derived from other parts of it. In vol. xlix. of the *Transactions of the Pathological Society of London* I described a cyst which I removed from the retro-peritoneal tissue of a young woman aged 20 years. The tumour was as large as an ostrich egg or a small cocoa-nut. It lay in front of the left ureter, just below the kidney. The cyst had a spherical cavity, filled with albuminous fluid, containing a quantity of fibrin, altered blood pigment, and cholesterol. During the removal of the cyst the lower part of the left kidney and the lower edge of the pancreas both came into view. But ovarian cysts are not always unilocular, and therefore it is not uninteresting to remark that I assisted my colleague, Mr Bowlby, to remove a multilocular retro-peritoneal cyst. The patient was a middle-aged woman, and, strangely enough, the cyst was situated in exactly the same place as the one which I have just described; that is to say, it lay upon the left ureter, just below the kidney. Referring again to the micro-photograph, it is to be noticed that lying close in front of the glomerular part of the suprarenal body is the developing pancreas; indeed, the organs are so close together, they are merely separated in the section by a large mesenteric vein. The cyst originating in the glomerular part of the suprarenal body would of necessity push forward the pancreas, and I should hardly doubt but that in this way a certain number of unilocular and multilocular pancreatic cysts may be explained.

Sometime ago, Dr Rolleston demonstrated adrenal structures low down in the hilum of the kidney. My observation proves that they are to be found far lower, and I venture to prophesy that they will ultimately be found round or within the epididymis itself.

Furthermore, at the earliest stages of development, the lower end of the Wolffian body is separated from that which ultimately becomes the urinary bladder by an inappreciable interval, and I would suggest that in this fact we may ultimately find the explanation of certain curious growths which seem to have originated betwixt the bladder and the rectum.

**SOME EXPERIMENTS ON BONE, WITH METHODS OF  
DEMONSTRATING THE CANALICULI.** By **WALTER  
COLQUHOUN, M.A., M.B., C.M.,** *Assistant to the Professor of  
Physiology in Glasgow University.*

ABOUT four years ago, when a student in Glasgow University, I began to experiment on bone, with a view to gain some information as to its mode of nutrition, and a more definite knowledge of the minute structure and arrangement of its canaliculi. My idea was to approach the subject by endeavouring to pass stains through the bone without decalcification, so that only the soft parts would become stained, and that by the natural channels. In a couple of months I had succeeded not only in passing any fluid through bone, but also in filling (or staining) the canaliculi with various precipitates.

The experiments were begun by soaking thin slices of bone in various staining fluids, but it was found that there was practically no penetration by the natural channels, even after considerable intervals of time. My next experiments were made by boring holes in the cancellated bone of the head of the femur, and allowing the bone to remain exposed to the air while the holes were kept filled with stain. The stains (picricarmin, eosin, saffranin, etc.) were found after some time to have diffused themselves through areas surrounding the holes, and those areas were cut into slices, which were dehydrated, passed through oil of cloves, then through canada balsam in benzole, after which they were transferred to slides with some thick canada balsam, and were left in a drying oven until the balsam was perfectly hard, and in a condition for grinding. After grinding, the sections showed that the stain had passed through the canaliculi, and that all the nuclei of the bone corpuscles were stained. The outlines of the canaliculi were, however, very faintly indicated. These experiments indicated the means by which fluids could be passed through bone, and the next step was to arrange glass tubing in lengths of about 12 feet up the wall of the laboratory. To the bottom of



each of these lengths of glass tubing a bone, such as the tibia of a sheep, was fastened by means of wide rubber tubing and india-rubber cork, after one end had been sawn off, and the medullary cavity cleaned out. The periosteum was also stripped, and any openings observed on the outside of the bone were plugged by small wooden pegs. The length of tubing was then filled with staining solution containing a little antiseptic, and the bone was left exposed to the warm air of the room, so that as it lost moisture from the outside, the stain would be sucked in by the natural channels. The experiments, after a lapse of time of about a month, succeeded perfectly, and all the nuclei of the bone were found stained, as also was the lining membrane of the canals, which in transverse section appeared homogeneous with sharp double outline, an appearance similar to that shown in section by the lining of a lacuna. Where the lining membrane of spaces or canals happened to become torn or rubbed off in spoilt sections which had not been sufficiently hardened, it showed in irregular patches, with apparently no preference for tearing in any particular direction. The matrix of the bone was quite unstained, and the outlines of the canaliculi were very faint.

All my sections were made by grinding after permeation by canada balsam, and they brought out very well the dense layer of calcified cartilage under the articular cartilage. This layer showed in my specimens rows of bodies perfectly black and opaque, four or five deep, arranged perpendicularly to the articular surface. On examination by reflected light, the bodies showed as white cells of oval shape, lying in a dense matrix. No processes in most cases could be detected, and the appearance was due to the fact that the cavities in which the cells lie was not permeated by the canada balsam, and being broken into in the process of grinding, the water used in that process penetrated the cavities, and led to the black opaque appearance. A point in which I was much interested, namely, the mode of nutrition of the articular cartilage, I have not been able to settle to my satisfaction. In all my experiments I have found it easy to get stain into the articular cartilage from the outside, but almost impossible to get any into it from the bone. The calcified cartilage below the articular cartilage is very dense,

and its nutrient arrangement is not at all well marked. The idea suggested itself to me that the nutrition of the articular cartilage may be due mostly, if not entirely, to the synovial fluid of the joint. The continual change of pressure would help the circulation very much, by setting up a pumping action by alternate compression and relaxation of areas of cartilage. The tendency to the formation of cartilage in joint cavities containing that fluid is well known pathologically, and a study of the situation, connections, and state of nourishment of such bodies might throw light on the subject.

After finding that I could make any fluid permeate bone, my next step was to remedy the faint staining of the canaliculi, and I determined to do so by using first a fixing fluid of penetrating power, to be followed by a fluid which would combine chemically with it and form a precipitate in the tissues. As in the former experiments, I worked first with slices of bone, since, although a staining fluid would not penetrate bone on prolonged soaking, there was no reason why chemical action should not have a penetrating effect. I used first bichromate of potash in 3 per cent. solution, with  $\frac{1}{4}$  per cent. osmic acid, as fixing fluid, but the osmic acid is not absolutely necessary, and the bichromate solution gives good enough results alone. The slice of bone was soon permeated by the fixing fluid, a few days being sufficient as a rule; and after grinding one side fairly smooth, the slice was transferred to 1 per cent. silver nitrate solution, and allowed to soak in a place screened from the light. After a week or two the slice was permeated with canada balsam, placed on a slide with the smooth surface down, dried in an oven and ground. It was found on grinding that the silver solution had penetrated only a certain number of layers of canaliculi; and when the grinding had reached the permeated layers next the slide, the section was quickly heated to soften the balsam, and then turned. The grinding was then continued until the section was a little thicker than one layer of corpuscles. In these preparations all the corpuscles and canaliculi were found stained black. Other fluids for fixing and staining were used, the only necessary conditions being that the fixing fluid must penetrate, and the second fluid form a dark precipitate with it. Thus mercuric chloride may be used to fix and dilute ammonium sulphide to

follow it. Some of the slices were decalcified by a mixture of acetic and chromic acids, so that thin slices could be obtained by cutting.

Many of the ground specimens were very instructive. Thus in some places the corpuscles, surrounded by their capsules, were torn out of their beds in the bone, the bed being indicated by an ellipse of different shading from the surrounding matrix. From the capsule appeared, sticking out, short processes, so that the corpuscle appeared like a small hedgehog. In other places transverse sections of processes showed clearly, under a power of 750 diameters, a black centre, surrounded by a double outline sharply defined, showing an appearance such as that displayed by a section through the capsule of a corpuscle, or the lining of a canal. In sections which showed that the cell substance was shrunken, and did not fill the lacunæ where they had been cut across, the large complete capsule could be seen in other parts torn out of its place, with the processes sticking out from it. All this seemed to indicate to me very clearly that there is a continuity between the lining membranes of canals, spaces, canaliculi, and lacunæ, and that what we call processes of the bone corpuscle are in reality hollow tubes, which are prolongations of the capsule. The canaliculi, which at one moment appear quite black, appear on the next instant as smooth glistening tubes on change of focus, and more particularly so where partial use is made of reflected light. The very methods which I had to take to stain the bone also point to the same conclusion. The canaliculi are very numerous on the borders of a canal, and one is lucky enough sometimes to see, where a canal lining has been shaved in longitudinal section, the black dots indicating their mouths. The same black dots are seen where processes have been shaved off from the capsule of a corpuscle which forms the lining of its lacuna. The silver nitrate method penetrates the layer of calcified cartilage below the articular cartilage very well, and brings out a lamellar arrangement parallel to the surface of the articular cartilage. The lamellæ are much wider than those of bone, and indicate, I take it, successive layers of matrix, each layer varying in density and degree of calcification throughout its thickness, following a somewhat regular plan, as shown by the graded shading. Without waiting

for permeation by silver nitrate, a beautiful specimen showing the lamellæ of bone may be obtained by the bichromate of potash and silver method. The action of the silver is allowed to go very little beyond the smooth surface of the section. That surface receives a few rubs on a smooth hone to remove the dead black from it, and being placed next the slide, the section is ground down to it. The interstitial substance between the lamellæ takes the stain the most.

To return to the nutrition of bone, it seems to depend, judging from the method of permeation by fluids, on the demand for fluid by the protoplasmic lining of the system of passages in the first place, and possibly on a protrusion or withdrawal of cell processes in the second place. Of the latter occurrence, however, I have no proof, and it seems to me quite unnecessary to assume a permanent protrusion of solid processes, such as may be seen given off from osteoblasts in the formation of bone, any more than it would be reasonable to assume the permanent impermeability of a process which may become hollowed out in the formation of a blood capillary. It is quite possible that, in the fresh state, the canaliculi may have more of the character of solid processes, but my contention is that at any rate they are potentially tubular, and that there is such a close connection between the external surface of the process and the matrix with which it is in contact that, at any rate after my manipulations, many of the processes show as tubes. The anastomoses which one notices also suggest the idea of hollow passages rather than solid processes. In a transverse section, if one regards the first circle of corpuscles, possibly four or five in number, surrounding a Haversian canal, one notices that the outline of the circle is quite definite, owing to anastomoses between the processes of corpuscles forming the second circle and those of corpuscles forming the first. The bodies of the corpuscles form a small proportion of the circumference of the first circle, and yet it is so definitely traced out that it almost presents the appearance sometimes of a circular canal, into which processes are opening on each side. By processes here, I mean of course what I consider to be tubular prolongations of the lining of the lacunæ.

It is interesting to consider the influences which, in my

experiments of passing fluid through bone, would tend to open or close the tiny mouths of the canaliculi opening into the canals. Loss of moisture, for example, by making lining membranes less swollen, and by causing retraction of processes, if there really are semi-fluid processes in the tubular prolongations of the corpuscular capsules, would cause opening of the ostia and passage of fluid. Pressure, on the other hand, by flattening a cushion-like membrane, would tend to close the ostia, and hence I depended on the slight pressure I used to cause passage of the fluid only, in conjunction with the drying which caused a demand for it.

It will have been noted that although I could not get stains to penetrate bone by soaking, yet where I used a fixing fluid of penetrating power, followed by a fluid which combined chemically with it, I got sufficient penetration of the latter for my purpose. As I have shown how to pass any fluid through bone, it follows that silver nitrate solution can be passed through a whole bone by the combination of pressure and drying, and that it may then be followed by bichromate of potash solution. Sections may then be cut and ground, or the bone may be decalcified by reagents, which will not dissolve the precipitate, for the purpose of cutting sections. For example, at the present moment I am engaged in passing gold chloride solution through a sheep's tibia, and I intend to decalcify thin slices afterwards by a mixture of formic acid with some ferrous sulphate. I hope in this way to obtain a finer coloration than that given by silver nitrate.

A great deal remains to be done yet at the subject, and I am resuming investigations after allowing the matter to rest for some time. In what has been done, I have to acknowledge my indebtedness to Professors Cleland and M'Kendrick for their kindly encouragement.

THE CARTILAGES OF THE MONOTREME LARYNX. By  
JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's  
College, Belfast.* (PLATES VII.-IX.)

As the generally accepted views regarding the phylogeny of the cartilages of the mammalian larynx are based to a large extent upon the peculiarities in the form, connections, and structure of these cartilages in the Monotremata, it is evident that an accurate knowledge of the anatomy of these cartilages is of fundamental importance.

Notwithstanding the contributions to this subject of Wiedersheim,<sup>1</sup> Dubois,<sup>2</sup> Walker,<sup>3</sup> Gegenbaur,<sup>4</sup> and Göppert,<sup>5</sup> there are still, I believe, various important points which have been inaccurately described or overlooked. This is partly due to the circumstance that the material at the disposal of those observers was small in amount, and generally imperfectly preserved. Further, the method of examination has been to a large extent confined to ordinary dissections, while the larynx both in the Echidna and in the Ornithorhynchus is so small that various points in the anatomy of the organ cannot be properly determined without the aid afforded by serial microscopic sections.

In addition to the dissection of an adult Ornithorhynchus and of an adult Echidna, I have mounted a complete set of serial sections of a young Echidna and of an adult Ornithorhynchus. I am greatly indebted to my friend Dr Gregg Wilson for generously placing at my disposal the two specimens of Echidna. The young Echidna, measured in a straight line from the front of the head to the most posterior part of the trunk, was 8·3 cm. long. Its body, however, was considerably curved

<sup>1</sup> *Grundriss der vergl. Anatomie der Wirbeltiere.*

<sup>2</sup> "Zur Morphologie des Larynx," *Anatomischer Anzeiger*, 1886.

<sup>3</sup> "On the Larynx and Hyoid of Monotremata,"—*Studies from the Museum of Zoology in University College, Dundee*, vol. i. No. 3, 1889.

<sup>4</sup> *Die Epiglottis*, 1892.

<sup>5</sup> "Ueber die Herkunft des Wrisberg'schen Knorpel," *Morphologisches Jahrbuch*, Bd. 21.

downwards in front and behind, so that along the median dorsal line from the tip of the nose to the end of the tail its length was 17.5 cm. The body was naked, the hairs and spines not yet having commenced to project from the surface.

In all my specimens the larynx was removed with a portion of the tongue, trachea, and pharynx. In the adult *Echidna* the distance from the tip of the epiglottis to the posterior end of the cricoid was 14 mm.; in the young specimen the length of the larynx after being embedded in paraffin was 4.5 mm. Allowing for some shrinking during the process, it was probably rather more than a third of the length of the adult organ. The larynx of the *Ornithorhynchus* is about the same size as that of *Echidna*. In my adult male it was 1.5 cm. long, and in the female 1.3 cm.

*Thyroid Cartilage.*—Undoubtedly the most important and interesting discovery in connection with the skeleton of the monotreme larynx was that made by Prof. E. Dubois. He found both in *Echidna* and *Ornithorhynchus* that the thyroid consisted of a small median piece, which was connected with two long and well developed pairs of cornua. The direction of these cornua was practically parallel with the posterior cornua of the hyoid, all of them passing from the ventral surface round the sides of the larynx with a distinct caudad inclination. From the appearance of the thyroid in the monotremes, Dubois based his theory that the mammalian thyroid is derived from the fusion of the cartilages of two pairs of visceral arches with one another, and with a median copula, or rather two copulae. The arches involved in this process are those immediately posterior to the hyoids, viz., the fourth and fifth post-oral. In his description Dubois states definitely that these five or six elements are continuous with one another, so as to form a single cartilaginous mass, but his illustration of the larynx of the *Ornithorhynchus* seen from the ventral aspect (see his fig. 7) might lead one to suppose that the median part was distinct from the horns. It is shaded differently, and separated from them by a fine line. Miss Mary Walker<sup>1</sup> in her paper describes and figures the larynx of both *Echidna* and *Ornithorhynchus* as though the cornua were not directly continuous with the copula, but articulated with it much in the same way as the two horns of the hyoid

<sup>1</sup> *Op. cit.*



the portal vein and depressing the action of the hepatic cells; or (5) by stimulating the intestinal glands, and thus producing drainage of the portal system, whereby the loaded liver might possibly be relieved."

Doubtless some drugs act by stimulating the muscular coat of the bile ducts and the intestinal mucosa, while others may act both on the bile ducts and the liver cells. I tried to ascertain if the secretion of bile would be affected by injecting certain drugs in solution directly into the circulation. If a drug injected into the external jugular vein increased the secretion of bile, the deduction, I think, would be that it stimulated the secretory cells of the liver.

### EXPERIMENT III.

A dog weighing 33 lbs. was put under ether. The capillary tube having been connected with the common bile duct in the usual way, a cannula was inserted into the external jugular vein, and the vein clamped below the insertion of the cannula. To save repetition, it may be stated that the subsequent experiments were carried out in a similar manner. Fifty c.c. of 0.9 per cent. chloride of sodium solution was injected into the vein, the dose being repeated after an interval of one hour. Afterwards a solution of Plattner's crystals was injected, and repeated after a further interval. (See Chart III.)

Chart III. shows a slight but unsustained increase after the first saline injection, and a distinct increase after the second injection, of Plattner's crystals. Probably the first injection of Plattner's crystals was too small to have an effect.

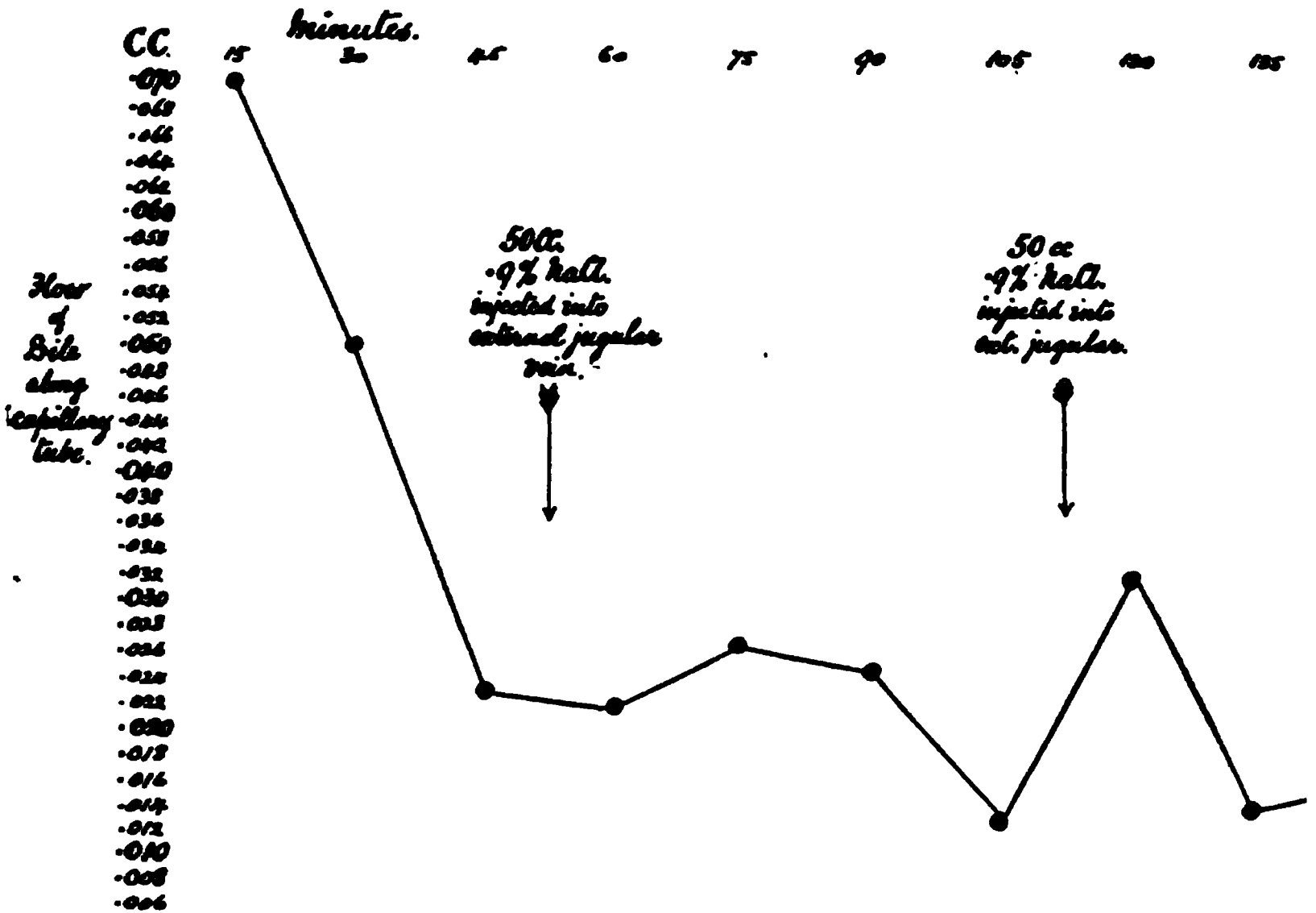
It is evident from this experiment that the injection into the circulation of 100 c.c. saline solution has little if any effect in accelerating the flow of bile, whereas a comparatively small dose of Plattner's crystals has a distinct effect.

### EXPERIMENT IV.

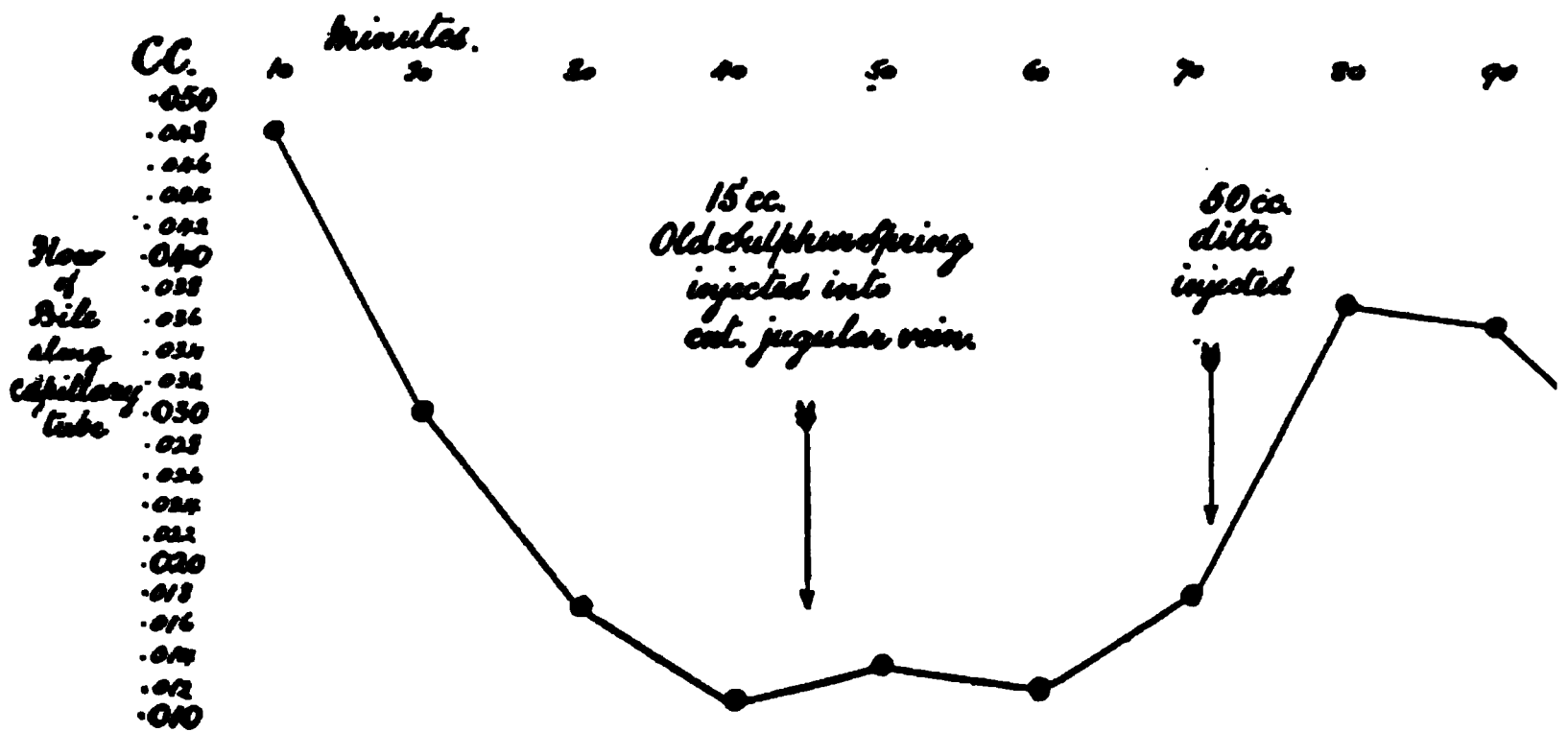
A dog weighing 14 lbs. was injected with 15 c.c., and after an interval 50 c.c. of strong sulphur water (Harrogate) at a temperature of 37° C. All the solutions were injected at the



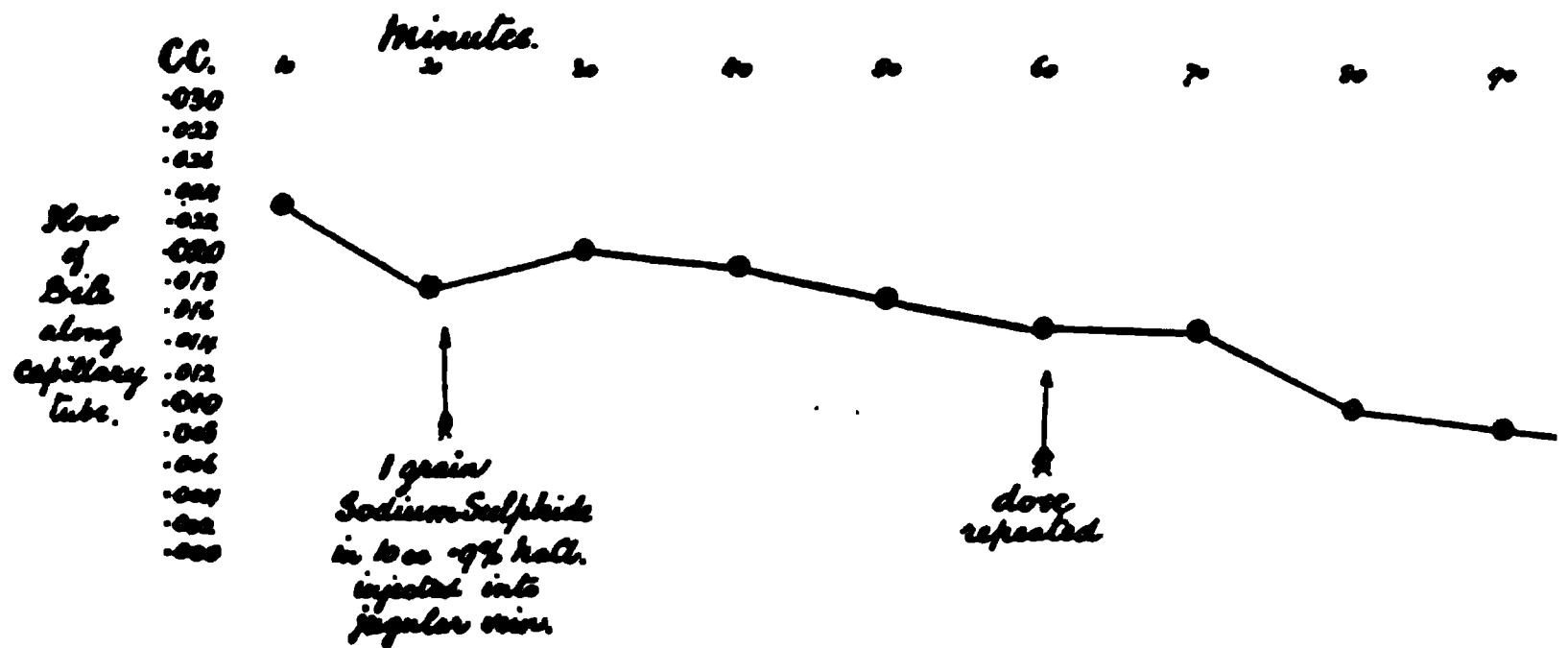
### Chart III.



### Chart IV.



### Chart VI.





same temperature. This substance was selected because in a previous investigation it was found to increase the flow of bile considerably. (See Chart IV.)

Chart IV. shows after the second injection a distinct and sustained increase in the rate of flow. In this case also probably the first dose was too small to produce an effect.

From this experiment, one is clearly justified in assuming that the sulphur water stimulates the secretory cells of the liver.

The next point I endeavoured to determine was the particular ingredient in the sulphur water which produced the increase in the rate of secretion. Sulphide of soda, magnesium chloride, and barium chloride were tried. The results are inconclusive.

#### EXPERIMENT V.

A dog weighing 15 lbs. was injected with 3 grains of sulphide of soda in 20 c.c. of a 0.9 per cent. saline solution, and after an interval a similar dose was given.

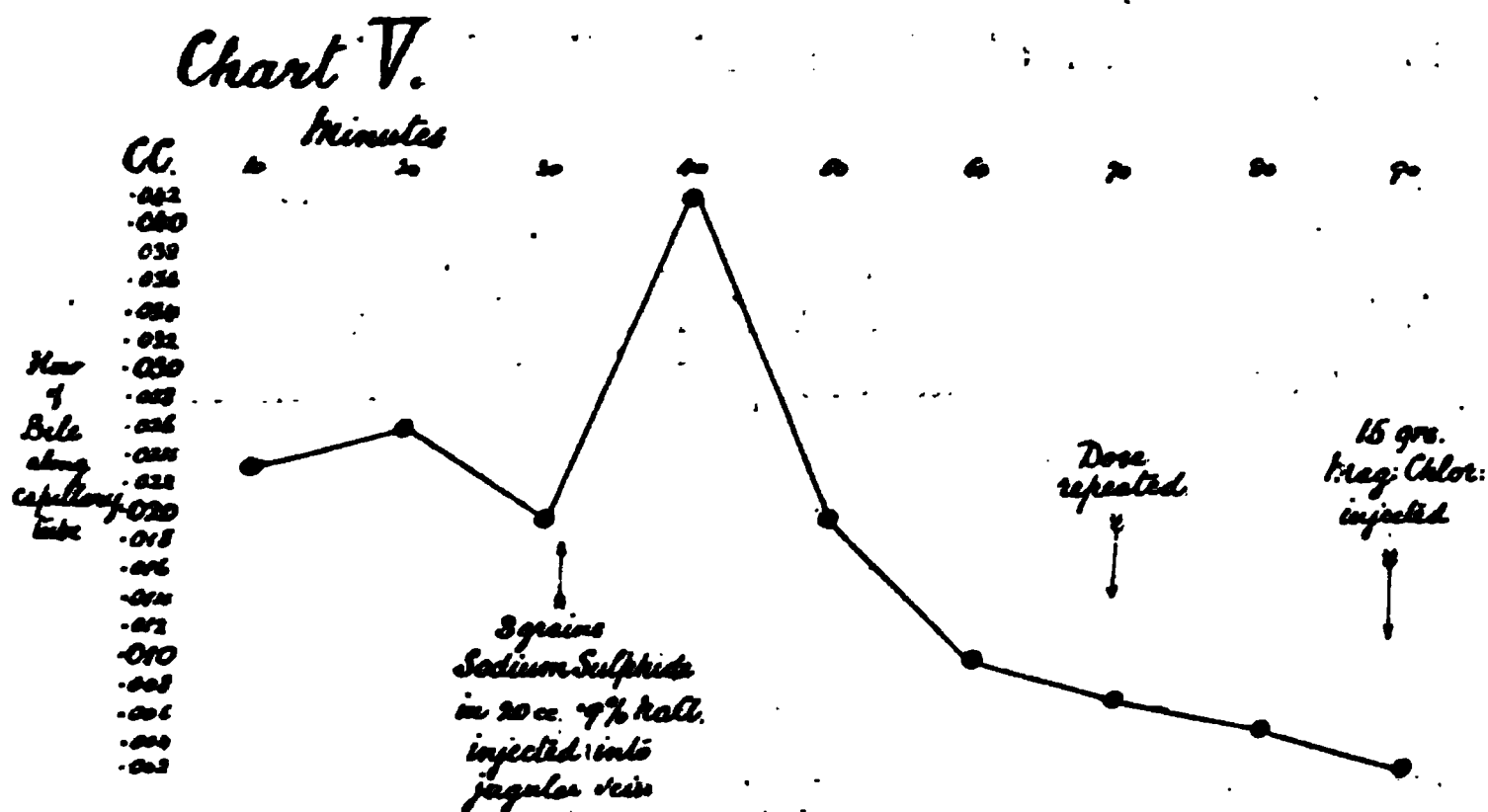


Chart V. shows a distinct rise after the first injection of the soda salt, but on repeating the dose no effect was observable. On injecting 15 grains of magnesium chloride the dog immediately died.

elastic fibres traversing the cartilage in all directions (Pl. VII. figs. 1, 2). A considerable number of the serial sections of the adult *Ornithorhynchus* were stained in the same way and gave similar results. The elastic fibres were larger and more abundant near the surface of the cartilage, but fine fibres could be traced round the cells in the centre of the cartilage. It is generally admitted that orcein is the best and most reliable test for the presence of elastic fibres. When the tissue has not been properly fixed, it is often impossible to stain these fibres with either picric acid or orcein. The failure of Gegenbaur to detect any elastic fibres in the epiglottis must have been due to the imperfect preservation of his specimens. Those who have investigated the minute structure of the marsupial and monotreme tissues are only too familiar with the difficulty of obtaining well fixed material.

It is well known that in the adult human subject small islands of hyaline cartilage are often found in the epiglottis and the cartilage of the external ear, and I have noticed well defined patches of hyaline cartilage in the cetacean epiglottis. In none of the three specimens of the monotreme epiglottis that I examined could I detect any such islands. This certainly favours the hypothesis that this formation of hyaline cartilage is a secondary product, and not the remains of a phylogenetic hyaline epiglottis.

The interesting problem raised by Gegenbaur as to the morphological significance to be attached to the histological structure of an organ, is one which in the present state of our knowledge cannot be adequately discussed. We know too little of the causes that give rise to a differentiation of the germ layers into the various tissues of the body, and of the influences that modify the structure of corresponding organs in different animals. Even with regard to the development of the various kinds of cartilage, authorities are by no means agreed. Some consider that the elastic fibres of elastic cartilage are a secondary product derived from a hyaline intercellular substance. According to more recent investigations, especially those of Spuler,<sup>1</sup> the elastic material is derived direct from the protoplasmic

<sup>1</sup> "Ueber Bau und Entstehung des elastischen Knorpels," *Sitzungsberichte der Physik.-medizin. Soc. in Erlangen*, 27 Heft, 1895.

processes of the cartilage cells. If this be true, elastic cartilage is not a mere secondary modification of hyaline cartilage, but is ontologically a distinct tissue.

In the case of the mammalian epiglottis the structure of its cartilage may fairly be considered of phylogenetic importance. As all the branchial arches are composed of hyaline cartilage, we might reasonably expect that any structure derived from them would possess, both in its ontogeny and phylogeny, a hyaline structure. On the other hand, should it differ in its texture from all the well known derivatives of these arches, we are entitled to suspect a different mode of origin. It appears to me, therefore, that the structure of the epiglottis is strongly opposed to Gegenbaur's theory of its being a derivation of a visceral arch.

Kallius<sup>1</sup> directs attention to the fact that the cartilage of the epiglottis differs from all the other great cartilages of the larynx in its late appearance. If it were formed from a branchial arch we should expect it to appear about the same time as the other derivatives of these arches. Its late development might be used as an argument in support of Dubois' hypothesis that it is a new formation.

The second main point advanced by Gegenbaur in support of his theory is, that the epiglottis is essentially a paired organ. He admits that the upper part of the cartilage of the epiglottis lying in the free fold of mucous membrane is a single piece, but he gives an illustration of the epiglottis of the *Ornithorhynchus* (see fig. viii.) to show that each half is concave, and thus shows a certain independence. Fig ix., in his memoir, representing two transverse sections of the epiglottis in the *Ornithorhynchus*, in each of which the cartilage consists of two lateral plates separated by a narrow interval, is apt to convey a false impression as to the extent to which the epiglottis is divided. The figure given by Göppert<sup>2</sup> of this cartilage in the *Echidna*, in which it has been removed from the larynx and spread out on a flat surface, is much more satisfactory. In both the monotremes fully three-fourths of the cartilage is single, only about the lower fourth being divided. I believe this basal division must be associated with the form of the laryngeal aperture,

<sup>1</sup> *Op. cit.*

<sup>2</sup> *Op. cit.*

which is a median cleft, bounded ventrally by the anterior part of the thyroid cartilage. The epiglottis lies almost entirely above this opening, but the two processes at its base extend into the lateral walls of the aperture. In the *Echidna* the apex of the epiglottic cartilage has a slight median notch, but this is absent in the *Ornithorhynchus*.

In the *Marsupialia*, the epiglottis, as Gegenbaur himself admits, shows at its base no trace of a division. It rests directly upon the anterior border of the thyroid, and takes no share in the formation of the lateral walls of the laryngeal orifice. Gegenbaur gives several illustrations of a basal division of the epiglottis in the *Rodentia*. I believe this is merely a secondary extension of the basal portion of the epiglottis into the lateral walls of the larynx. In probably the great majority of mammals the base of the epiglottis is broad and flat, or shows a median process directed backwards towards the thyroid.

Kallius,<sup>1</sup> in describing the development of the human epiglottis, writes as follows:—

“Bei ihr ist an keiner Stelle irgend welche Andeutung einer paarigen Anlage zu sehen” (s. 346).

The evidence derived from comparative anatomy and from development appears to me to show that the cartilage of the epiglottis is an unpaired median structure, and gives no support to Gegenbaur's theory that it is derived from the union of two lateral elements. If it were formed from the 6th arch, one would expect to find some evidence of a connection with the caudal end of the thyroid, yet even in such low forms as the marsupials it rests upon the cranial border of the thyroid, and does not extend on to its ventral surface. It is true that the branchial arches tend to overlap one another from before backwards, but in no other case is there any proof of one arch shifting its position so far forwards as to lie anterior to two arches which primarily are in front of it.

*Cricoid Cartilage* (Pl. VIII., IX. figs. 3, 4, 5).—In my specimens of the *Echidna* this cartilage does not form a complete ring, being deficient dorsally, while in the *Ornithorhynchus* the ring is complete, thus presenting a higher degree of development than in the *Echidna*. These results agree with those of Walker, but

<sup>1</sup> *Op. cit.*

Dubois figures the cricoid of the *Ornithorhynchus* as deficient posteriorly. It is to be noticed, however, that in this animal the dorsal aspect of the cricoid has a deep median notch reaching from the posterior border nearly to the anterior end, so that the ring in this situation is narrow.

The anterior border of the ventral portion of the cricoid possesses a median process, which I found in my serial sections of an adult *Ornithorhynchus* to extend slightly on to the dorsal aspect of the thyroid cartilage. This process gives origin to the thyro-crico-arytenoid muscle, and is connected anteriorly to the septum, from which the more anterior fibres of the same muscle spring. Gegenbaur has a view of the ventral aspect of the larynx of the *Ornithorhynchus* (see his fig. 8) with the thyroid cartilage removed. He shows this process of the cricoid, but figures and describes it as reaching forwards to the base of the epiglottis. My sections give no support to this view.

*Arytenoid Cartilages* (Pl. VIII. figs. 3, 4).—These cartilages are well developed, but do not attain such a relatively large size as in some of the Marsupialia. Their shape and relations closely correspond to the marsupial type, of which I have already given an account in this *Journal*.<sup>1</sup> The median processes of the two cartilages articulated with one another, and their apices reached forwards to the laryngeal orifice.

*Interarytenoid and Intercricoid Cartilages*.—In the dorsal wall of the larynx there are two small median pieces of hyaline cartilage which have received various names, and rarely an accurate description.

The interarytenoid (Pl. VIII. fig. 3) is the more anterior of the two, and corresponds to the interarytenoid cartilage which I have always found in the Marsupialia. As in the marsupials, it separates the fibres of the arytenoid muscle into two lateral portions which are attached to its sides. It lies anterior to the united internal processes of the arytenoid cartilages (Pl. VIII. fig. 4), and also extends slightly on to their dorsal aspects. Dubois called this the anterior procricoid, but I have already given my reasons for preferring the term 'interarytenoid,' which I believe was first used by Luschka.

The intercricoid cartilage is not found in the Marsupialia, at

<sup>1</sup> "The Marsupial Larynx," vol. xxxiii.

least so far as my observations go. It is the posterior procricoid of Dubois. In my young *Echidna* it was a spherical piece of cartilage, with a diameter of .25 mm. It was situated in the interval between the lateral portions of the cricoid (Pl. IX. fig. 5), at the anterior and narrowest part of the notch. In the adult *Ornithorhynchus* the cricoid formed a complete ring, and the cartilaginous nodule was found in the notch on the dorsal part of this cartilage, *posterior* to the place where the ring was completed.

Nothing is known regarding the morphology of these two small bodies.

The majority of the observations upon which this paper is based were made in the Anatomical Institute of the Munich University, and I desire to acknowledge the great kindness of Professor C. v. Kupffer, who afforded me every facility for my investigations.

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#### DESCRIPTION OF PLATES VII.-IX.

Fig. 1. Transverse section through free projecting part of epiglottis of an adult *Ornithorhynchus*, stained with orcein. (*a*) mucous membrane on dorsal aspect; (*b*) glandular tissue; (*c*) cartilage.

Fig. 2. Section of same epiglottis further back.

Fig. 3. Transverse section of larynx of a young *Echidna*. *cr*, cricoid cartilage; *th*<sup>2</sup>, posterior cornu of thyroid cartilage; *th*<sup>1</sup> and *h*<sup>2</sup>, anterior cornu of thyroid and posterior cornu of hyoid united with one another; *a*, arytenoid cartilage; *ia*, interarytenoid cartilage.

Fig. 4. Transverse section of same larynx as fig. 3, but further back; lettering as in fig. 3. The two arytenoid cartilages are seen articulating with one another by their internal processes.

Fig. 5. Transverse section posterior to fig. 4. Same lettering as in figures 3 and 4. *ic*, inter-cricoid; *th*<sup>1</sup> and *h*<sup>2</sup> are posterior processes of the single plate of cartilage seen in figures 3 and 4.





FIG. 1.



FIG. 2.





1.2    a    h<sup>2</sup> /

FIG. 3.

FIG. 4.



i. c. h<sup>2</sup>

FIG. 5.



## A COMPARISON OF THE PELVIC VISCERA AND THE PELVIC FLOOR IN TWO ADULT MALE SUBJECTS.<sup>1</sup>

By JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's College, Belfast.*

COMPARATIVELY few observations have been published on the extent of the variations in the position of the bladder, rectum, and pelvic peritoneum as seen in different individuals under somewhat similar conditions. This is also the case in connection with the degrees of thickness of the pelvic floor.

Theoretically, there must be a decided tendency to the occurrence of such variations. During the periods of development and growth marked changes take place in the position of the bladder and the rectum, and any arrest or excess of these movements will affect the position of these organs in the adult. Further, the pelvic floor is made up largely of muscles and fat, and no structures in the body vary more in their amount. Such theoretical deductions are confirmed by a comparison of the two specimens (see figs. A. and B.) now to be described.

Subject A (male), aged 27 years, rather thin, muscular system of average development, and general form of body normal.—As this subject was selected for class demonstrations on the topography of the abdominal viscera, it was hardened by the injection of a solution of formal before being brought into the dissecting-room. When the peritoneal cavity was opened, and the coils of the intestine lying in the true pelvis were removed, the rectum was found empty and contracted, while the bladder was relaxed, and contained only a very small quantity of urine. On digital examination of the recto-vesical pouch of peritoneum, the vasa deferentia, the vesiculæ seminales, and the prostate gland were easily felt through its anterior wall. By keeping one hand in the pelvis, and passing a finger of the other hand through the anus, it was readily ascertained that the recto-vesical pouch reached downwards nearly to the upper end of

<sup>1</sup> Read at a meeting of the Anatomical Section of the Royal Academy of Medicine in Ireland on 3rd Feb. 1899.

*Fig A*

FIG. A.—Median section of pelvis of subject A. Reduced by photography from life-size drawing.



—  
FIG. B.—Median section of pelvis of subject B. Reduced by photography  
from life-size drawing.

the anal canal, or perineal portion of the rectum. In order to make a more careful study of this specimen the entire pelvis was removed and placed in a 5 p.c. solution of formal. To ensure a thorough hardening of the bladder, 200 c.cm. of formal solution was injected through a ureter into its cavity. After being kept several weeks in this fluid the pubic symphysis and the pelvic contents were divided with a knife in the median plane, and the section of the pelvis was completed by sawing through the sacrum.

Subject B, about 40 years old.—For comparison with the above, I have selected the section of an adult male pelvis which has been in my collection for several years, and a drawing of which will be found in *Quain's Anatomy*, 10th edition, vol. iii. pt. 4, p. 114. The body from which this specimen was prepared was hardened by the injection of Müller's fluid, and subsequently of spirit. The section was made, as in subject A, with a knife and saw, after the tissues were thoroughly fixed. The greater part of the rectum was empty and contracted, but just above the anal canal it contained some fæces. The bladder was moderately contracted, and held about 100 c.cm. of urine.

These subjects were both of average height, and the size of their bony pelvis almost identical. Thus the conjugate of the pelvic inlet was 10 cm. in each case. The outlet was 7·6 in A, and 8·2 cm. in B. This slight difference apparently depended upon a greater development of the sub-pubic ligament in A and the coccyx being turned rather more forwards. The sacrum in A, however, was more concave from above downwards, so that the antero-posterior extent of the pelvic cavity was greater than in B. The anterior surface of the sacrum and coccyx, measured in the median plane, and following their curvatures, was 7·6 cm. in A, and 8·2 cm. in B. Müller's fluid, employed for the hardening of subject B, is very liable to distend the subcutaneous and submucous connective tissue when injected into the vessels, but this distension disappears, at least to a large extent, when the hardening is completed, as in this case, by spirit.

The principal differences between these two bodies were, that A was thin, and almost destitute of subcutaneous fat, while B

had a better muscular development, and his adipose tissue was abundant.

*Bladder.*—This organ was relaxed and nearly empty in A, and about 200 c.cm. of formal solution was injected into its cavity through one of the ureters; in B it was moderately contracted, and contained 100 c.cm. of urine.

In specimen A the bladder was situated entirely in the true pelvis, and no part of it reached a point nearer than 17 mm. from the plane of the pelvic inlet; while in B, although it did not contain so much fluid, a small portion of its wall projected 1 cm. above this plane.

The urethral orifice is a convenient point to select in estimating the position of the basal portion of the bladder. It must be remembered, however, that this orifice, although more firmly fixed than the other parts of the bladder, is still subject to considerable displacement. Thus Garson<sup>1</sup> and others have shown that distension of the rectum pushes it upwards and forwards; and I<sup>2</sup> have endeavoured to prove that during distension of the bladder the urethral orifice is depressed, and the prostatic portion of the urethra shortened.

The opening of the urethra in A was 6.5 cm. from the nearest point on the conjugate of the pelvic inlet, and in B 4.4 cm. According to Disse<sup>3</sup> the average distance is 5.5 cm. In A the orifice was 12 mm. below a horizontal line passing backwards from the upper body of the pubic symphysis, while in B it was only 3 mm. Disse gives 5.5 cm. as the average distance between the upper border of the pubic symphysis and the urethral orifice; in A it was 7.0 cm., and in B 5.0 cm. From these measurements it is evident that the urethral orifice is higher up and farther forwards in B than in A, and that the difference is more marked in the antero-posterior than in the vertical direction.

The urethral orifice is generally regarded as the lowest part of the interior of the bladder, and such is usually the case. In A, however, the most dependent part is situated in front of the

<sup>1</sup> "Die Dislocation der Harnblase und des Peritoneum bei Ausdehnung des Rectum," *Arch. f. Anat.*, 1878.

<sup>2</sup> "The position of the empty and distended bladder in the male child," *Edinburgh Medical Journal*, April 1885.

<sup>3</sup> "Untersuchungen über die Lage der menschlichen Harnblase und ihre Veränderung im Laufe des Wachstums," *Anatomische Hefte*, Heft 1, 1891.

prostate and behind the pubic symphysis. Professor Wardrop Griffith recently showed me a section of an adult male pelvis in which the same condition existed. In both these cases the subjects were very thin, and I am inclined to attribute this depression to the absence of the retro-pubic pad of fat. Of course other conditions, such as enlargement of the prostate, may alter the relative levels of the urethral orifice and of this part of the bladder.

*Curve of Urethra.*—The most striking difference in the curvature and direction of the urethra between A and B is that in the latter the urethra passes from the vesical orifice straight downwards and backwards through the prostate gland, and in the membranous portion turns rather abruptly downwards and forwards, while in A this change in the direction of the urethra occurs about the middle of its prostatic portion. It is easily conceivable that a distension of the lower part of the rectum in A, by pushing upwards and forwards the prostate and the bladder, would cause its urethra to assume a direction very similar to that of B.

*Rectum.*—Down to the level of the middle of the third piece of the sacrum, the rectum in A had a thin and long mesorectum, and was consequently freely movable. Below this it became fixed to the sacrum, devoid of peritoneum on its posterior aspect, and was placed almost entirely to the left of the mesial plane as far as the tip of the coccyx, but where it rested on the ano-coccygeal body it was median in position. The whole length of the rectum was empty and contracted. In B the median section exposed the cavity of the rectum from the level of the lower border of the 2nd sacral downwards to its termination, and above the part shown in fig. B it had a mesorectum, the two peritoneal layers of which were separated by a quantity of fat. There was also a considerable amount of fat separating the rectum from the anterior aspect of the lower part of the sacrum and from the coccyx. The facility with which even a slight amount of faeces in the ampulla of the rectum can push forwards the anterior part of this space so as to bring it into close relation with the membranous portion of the urethra is well shown in this subject. Thus the thickness of the tissue between the cavity of the rectum and the lumen of the urethra

is only 5 mm. In A, where this part of the rectum was empty and its lumen in the form of a transverse slit, the distance between the two cavities was 2.3 cm. These relations are of interest in connection with the well known clinical fact that faeces in the lower part of the rectum may interfere with micturition, and they also show how the mobility of this part of the rectal wall allows a catheter in the membranous portion of the urethra to be felt so readily per rectum.

*Peritoneum.*—In A this membrane is in contact with the upper and posterior surface of the symphysis for a distance of about 13 mm. before passing backwards to the bladder, while in B the peritoneum did not reach the pubic symphysis, being reflected from the anterior abdominal wall on to the bladder 10 mm. above its upper border. The difference, however, is still more marked in connection with the levels of the respective recto-vesical pouches. Thus in A the bottom of the recto-vesical pouch is 2 cm. below the level of the upper part of pubic symphysis; it corresponds to a line uniting the lower edge of the pubic symphysis with the tip of the coccyx, and is 3.5 cm. from the middle of the anal orifice. In B this pouch is 1 cm. above the level of the top of the pubic symphysis, 3.6 cm. above plane of pelvic outlet, and 8 cm. from the anus. The relations of the peritoneum in B are nearly identical with those of an adult male shown in plate 1 of Braune's *Topographisch. Anatomischer Atlas*. As the bladder contained only about 100 cm. of urine and the rectum was nearly empty, the peritoneum was probably a little higher than usual for such states of the bladder and the rectum. The fat, however, which was situated behind the rectum probably compensates for the slight distension of this organ. Waldeyer<sup>1</sup> gives the height of this pouch above the anus as 5 to 6 cm. In Braune's section it is 7.8 cm. and in my specimen B 8 cm., so that Waldeyer's estimate is too low for subjects in which the muscular and adipose tissues are fairly well developed. Traeger<sup>2</sup> gives 5.5 cm. and 10.8 cm. as the two normal maxima, and such a range of variation is not too great.

<sup>1</sup> *Das Becken*, p. 279.

<sup>2</sup> "Ueber abnormen Tiefstand des Bauchfelles im Douglas'schen Raume beim Manne," *Arch. f. Anatomie*, 1897.

In A the peritoneum is undoubtedly abnormally low, even for a thin subject with an empty rectum. This remark applies especially to the recto-vesical pouch which reaches down to the plane of the pelvic outlet, and is only 3.5 cm. from the anal orifice. The peritoneum reached even lower than this when the bladder was empty, as it was raised somewhat by the injection of 200 c.cm. of formalin solution into the bladder. Such a lower position of the recto-vesical pouch is of embryological and of surgical interest. In an embryo 35 mm. long Zuckerkandl<sup>1</sup> found that the coelom extended caudad between the hind gut and the Wolffian ducts to a point distinctly beyond the union of the sexual and urinary ducts, and he states that until about the middle of foetal life the rectal aspect of the prostate is completely covered by peritoneum. In the newly-born child the peritoneum usually reaches as low as the upper border of the prostate, and sometime covers it slightly. The persistence in the adult of such a deep recto-vesical pouch as is found in the young foetus does not appear to be common, but Traeger<sup>2</sup> has recently described a case in which the recto-vesical pouch extended to within 2.5 cm. of the anus. In Traeger's paper will be found the literature of the cases of so-called hernia of the recto-vesical pouch, and a discussion as to whether they are congenital or acquired. The fact that cases of abnormally deep recto-vesical pouches do occasionally occur is obviously of importance to the surgeon in connection with various operations on the rectum and the base of the bladder.

*The Pelvic Floor.*—This term is a convenient one for the mass of tissue which closes the pelvic outlet, and upon which the pelvic viscera rests. Owing to its connection with these viscera it is not easy to define precisely its upper limbs, but on the whole the recto-vesical layers of the pelvic fascia may most conveniently be regarded as representing the level of its upper boundary. This floor forms a compact mass, which serves to support the superincumbent organs, and is traversed by certain slits or faults, the walls of which are normally in contact, but can be separated to permit of the passage of the genito-urinary products and of the excreta from the alimentary canal. In the

<sup>1</sup> "Beiträge zur Lehre von den Brücken im Bereiche des Douglas'schen Raumes," *Deutsche Zeitschrift für Chirurgie*, 1891.

male these clefts are the urethra and the anal canal, while in the female it is still further weakened by the addition of another fault—the vagina. In consequence of the important part played by the pelvic floor in parturition, and its liability to fail as a supporting structure, special attention has been directed to its structure and functions in the female, more particularly by Berry Hart, and other obstetricians and gynecologists. In the male it is only in the region of the anal canal that prolapse is liable to occur, the anterior portion of the pelvic floor being very thick and compact, and its cleft—the urethra—too small to constitute a source of weakness. Nevertheless, the thickness of the male pelvic floor and the relations of its constituent parts are of great importance in various surgical operations in the perineum. Both surfaces of the pelvic floor are very uneven, and some difficulty is experienced in the selection of suitable points from which to measure its thickness. The bladder, although intimately attached to the floor, must be regarded as resting upon it, while the prostate gland is embedded in it. The part of the second portion of the rectum which is situated in front of the coccyx rests upon the ano-coccygeal portion of the pelvic floor, and upon the lateral walls of the upper end of the anal canal. Both the rectum and the bladder serve as reservoirs in which material can be collected and retained, while the urethra and the anal canal are normally closed, and only open temporarily to allow of the discharge of the contents of the bladder and rectum. For this reason I prefer the term ‘anal canal’ to that of ‘3rd or perineal portion of the rectum.’ In a median section of the male pelvis the thickness of the anterior portion of the pelvic floor may be conveniently estimated by the distance between the urethral orifice of the bladder and a point on the skin of the perineum vertically below this. In the comparison of sections A and B, I have selected the under surface of the bulb of the corpus spongiosum, so as to eliminate the amount of subcutaneous fat. In A the distance between these two points is only 3·7 cm., while in B it amounts to 6·4 cm. We have already seen that the internal urinary meatus is higher in B than A, and it may also be observed that the under surface of the bulb is further below the plane of the pelvic outlet in B than in A, so that the greater

thickness of the pelvic floor in B as compared with A is due both to the floor extending higher up and to the pelvic cavity, and also to its projecting further downwards below its outlet. The thickness of the pelvic floor in the median plane can be measured by the length of the anal canal or of the internal sphincter. In A this is 2·3 cm., and in B 3·3 cm. A comparison of the two sections also shows that the mass of tissue between the anus and the coccyx is distinctly thicker in B than in A, and that the coccyx is much nearer the cutaneous surface in A than in B.



**A NEW OSTEOMETRIC BOARD.** By **DAVID HEPBURN, M.D.,**  
*Lecturer on Regional Anatomy, University of Edinburgh.*

AN Osteometric Board is an apparatus for determining the length of such bones as are too long or too unwieldy for measurement by an ordinary callipers. The apparatus in current use was designed by M. Broca, and consists of a flat graduated board or plank, at one end of which a flat vertical upright is fixed. Against this upright part the bone to be measured is placed, while to the opposite end of the bone a right-angled triangle of wood is applied, and the length of the bone is read off upon the graduated plank. The chance of error is so constant that scarcely any two observers can obtain the same reading, nor can the same observer readily obtain the same reading on two successive attempts without a considerable amount of careful management, because it is extremely difficult to apply the edge of the movable upright to the most prominent part of the end of a rounded bone such as the head of the femur.

As it is quite evident that this personal error should not exist in the case of such an object as an unvarying and rigid

**Hepburn's New Osteometric Board.**

bone, I have devised the board which is shown in the accompanying illustration.

It consists of a horizontal mahogany plank, graduated upon each of its lateral margins by boxwood scales into both millimetres and the English inch subdivided in tenths. It is very advisable to have both French and English measurements side by side, as it avoids the necessity for calculations on the many occasions in which it is most convenient for English-speaking people to represent a figure in their own system, as, for example, in recording the height of a man. At both ends, uprights are fixed in a vertical transverse position, between which there extend two parallel brass rods. These rods pierce a third intermediate vertical shutter, which may be moved to and fro upon the brass rods. At the points where the rods pass through the movable shutter they are made to traverse short pieces of brass tubing, which are firmly fixed to the upright. In this way all appreciable error from oscillations of the upright is prevented, and it is impossible to obtain discrepant readings from separate measurements of a bone. Moreover, the measurement can be obtained with great speed as well as with great exactness, no matter who uses the instrument.

The apparatus is useful for ascertaining the greatest width and height of an articulated pelvis, two measurements which are very troublesome to obtain by callipers, because of the peculiar shape and somewhat unwieldy nature of the pelvis.

It is not intended to supersede the use of callipers for those measurements for which they are most suitable.

Its strength and solidity are points in favour of the apparatus, since it is entirely intended for use in the laboratory.

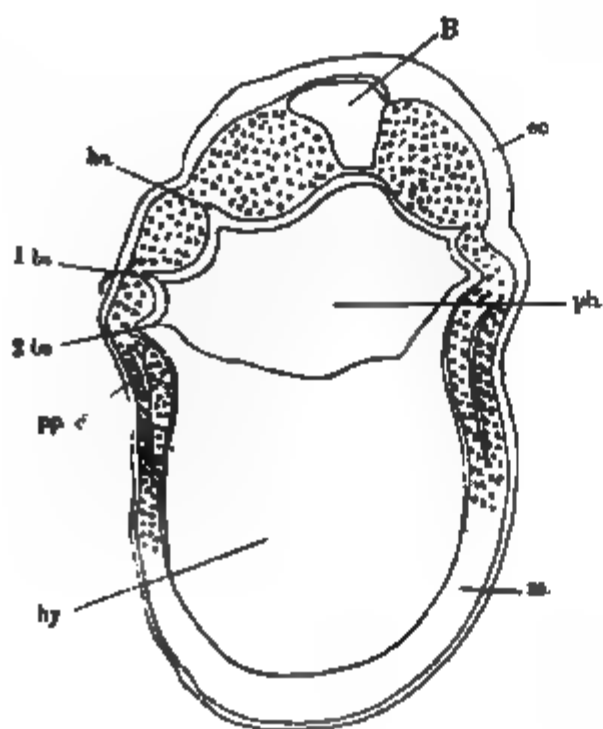


Fig. 1.

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Fig. 2.

4  
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Fig. 3.

E

Fig. 5.  
MR EDGEWORTH on Medullated  
Fibres of Cranial Nerves.

Fig. 4.



1 11 \ 1

Fig. 7.

Fig. 6.

Fig. 8.

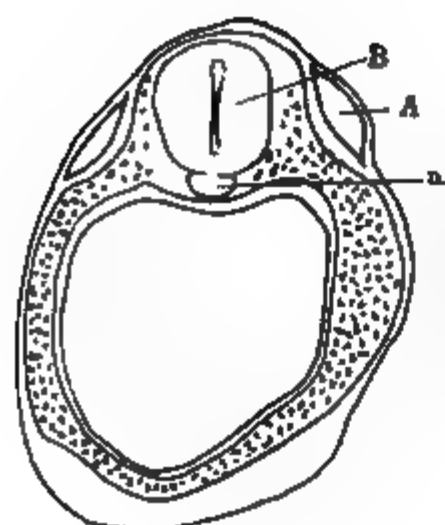


Fig. 9.

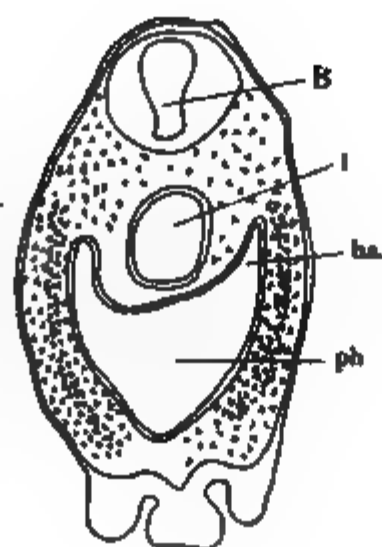


Fig. 10.

Fig. 11.



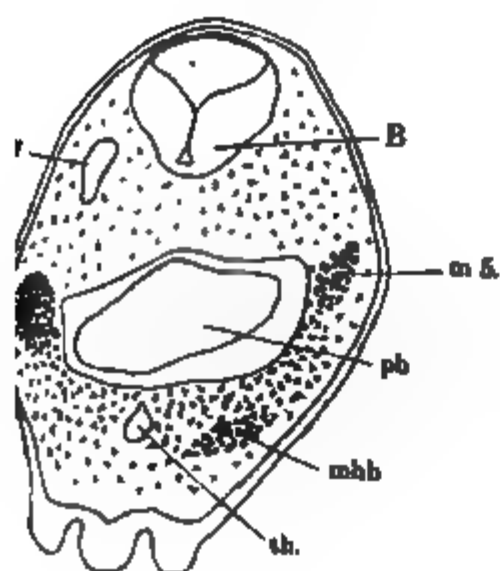


Fig. 12.

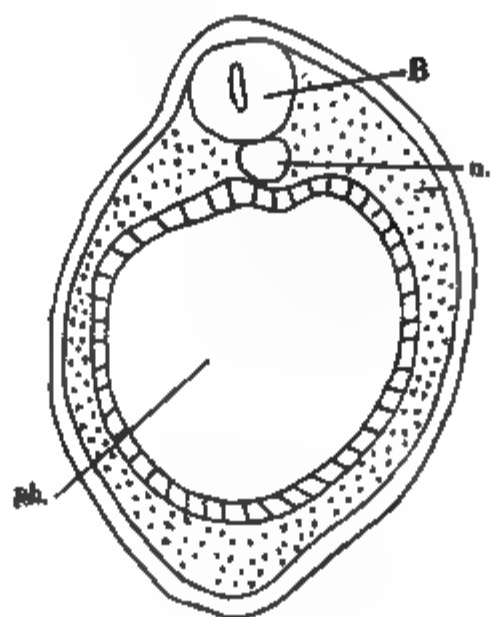


Fig. 13.



Fig. 15.



Fig. 16.



Fig. 18.



Fig. 14.

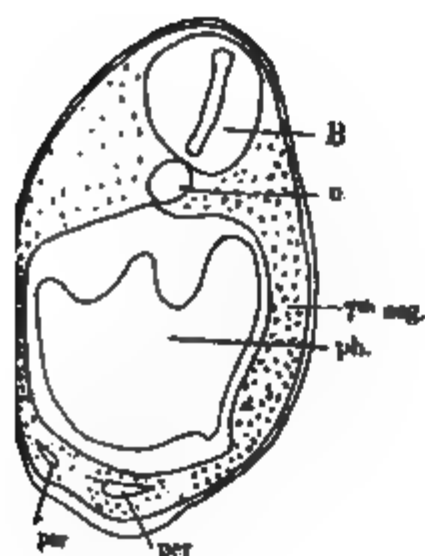


Fig. 17.

Fig. 19.

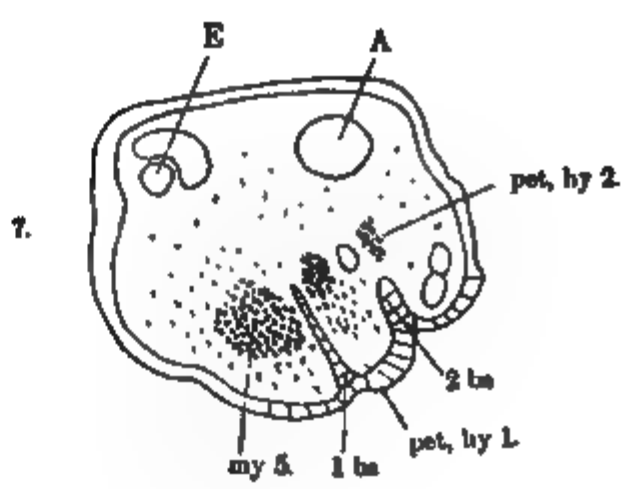


Fig. 20.





v      VII

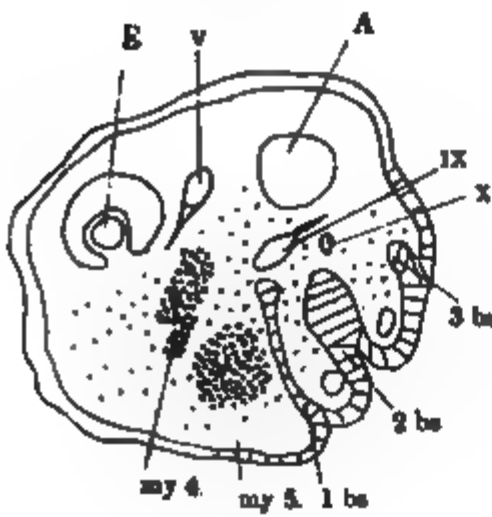


Fig. 21.

Fig. 22.

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Fig. 23.

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Fig. 24.

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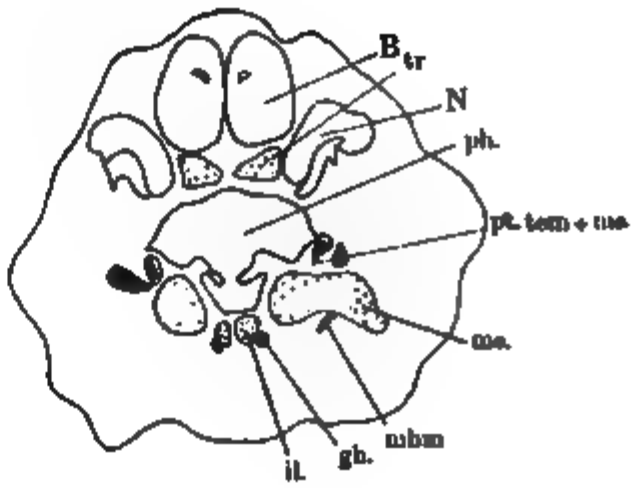


Fig. 26.

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Fig. 25.



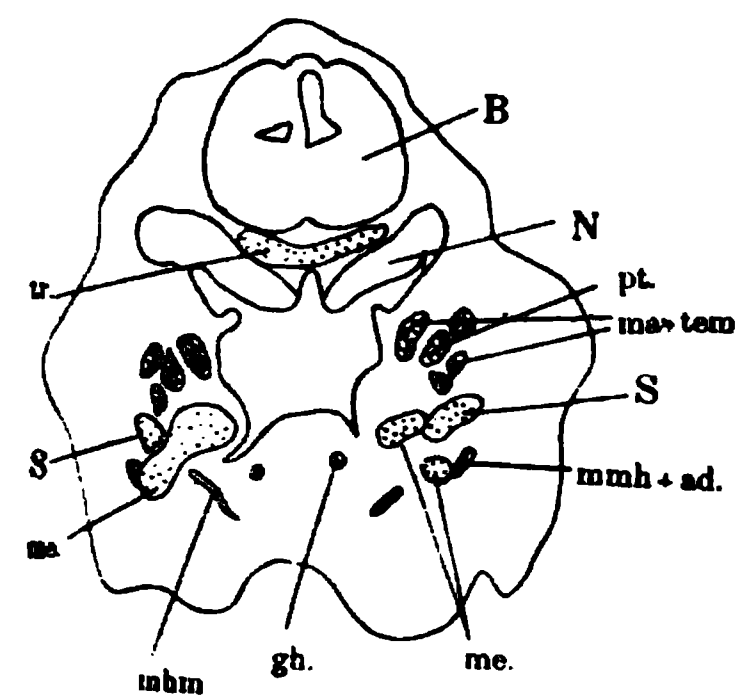


Fig. 27.

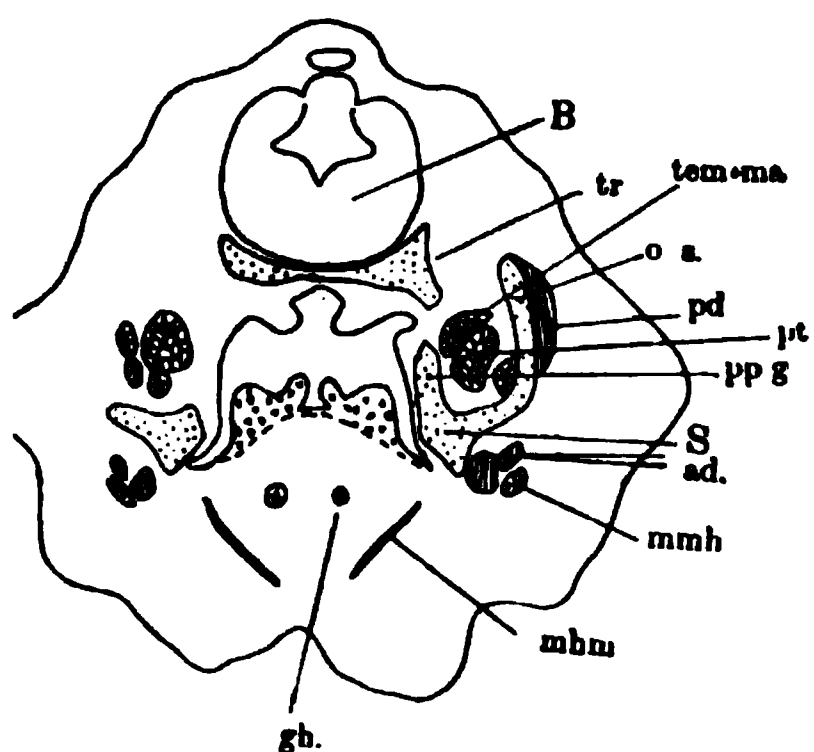


Fig. 28.

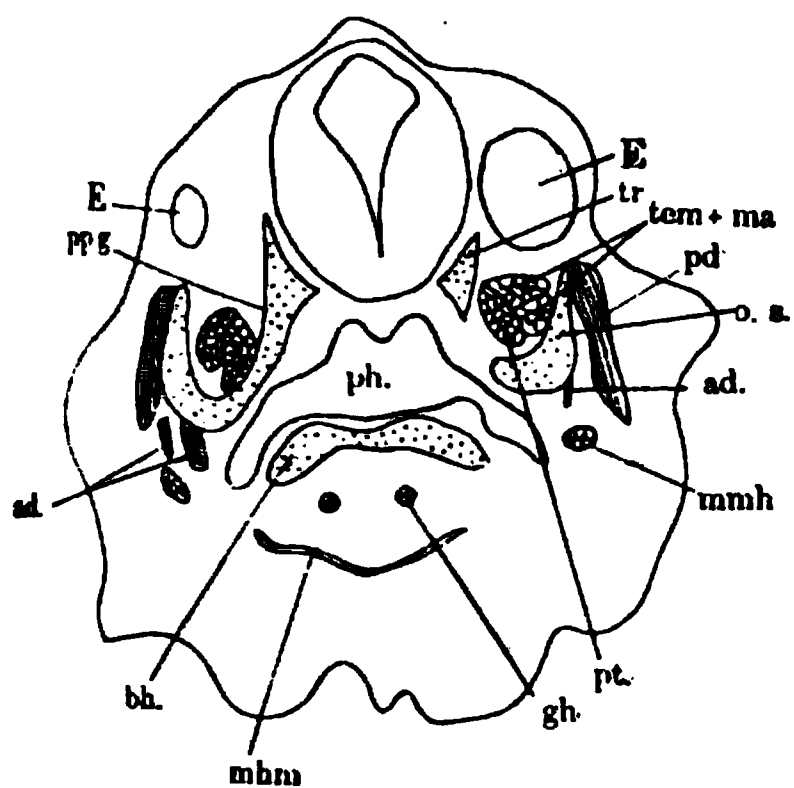


Fig. 29.

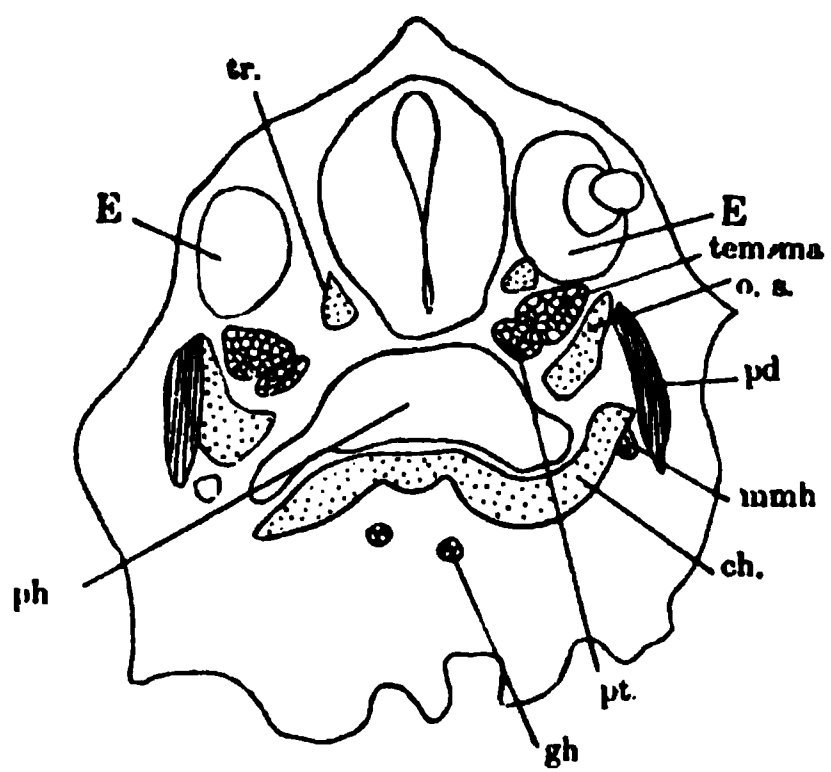


Fig. 30.

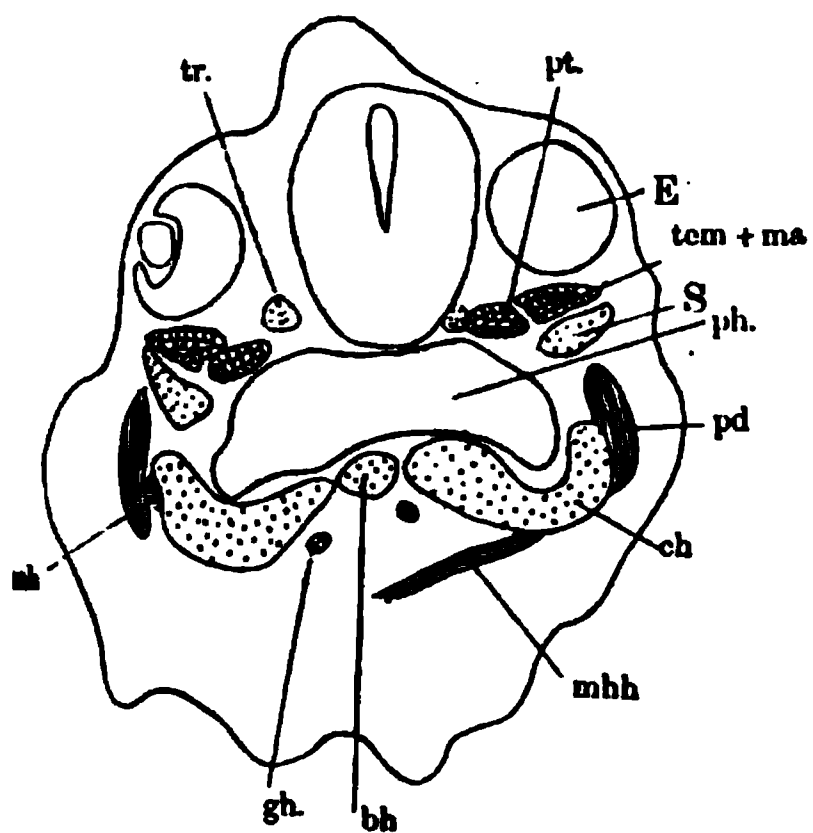


Fig. 31.

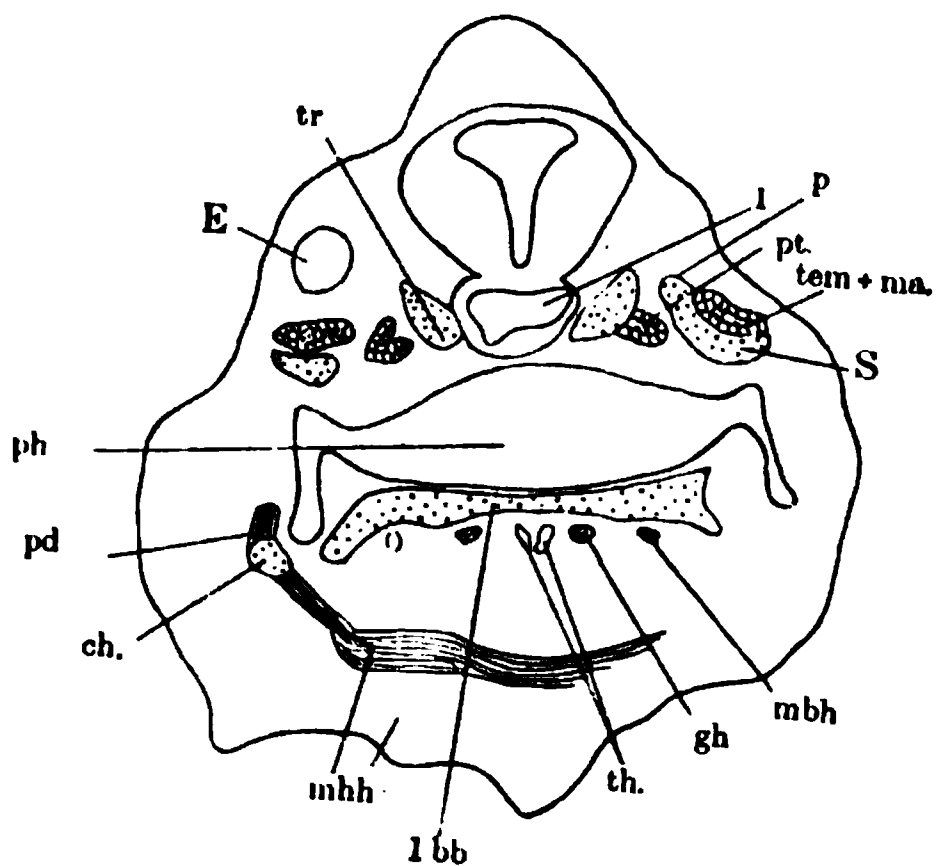


Fig. 32.



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Fig. 33.

  
Fig. 34.

Fig. 35.

Fig. 36.  
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Fig. 37.


  
Fig. 38.

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Fig. 39.

  
Fig. 40.



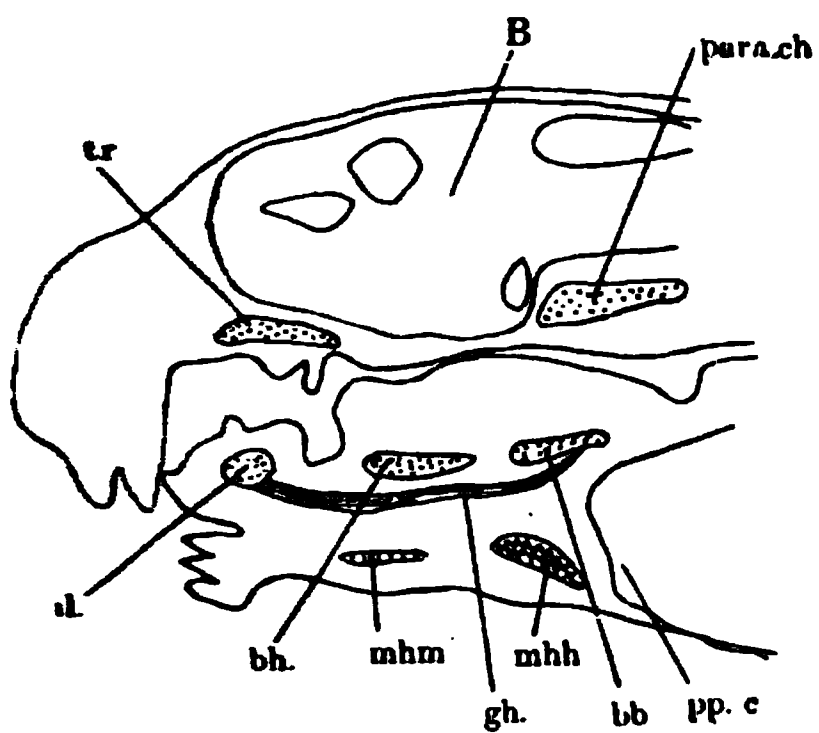


Fig. 41.

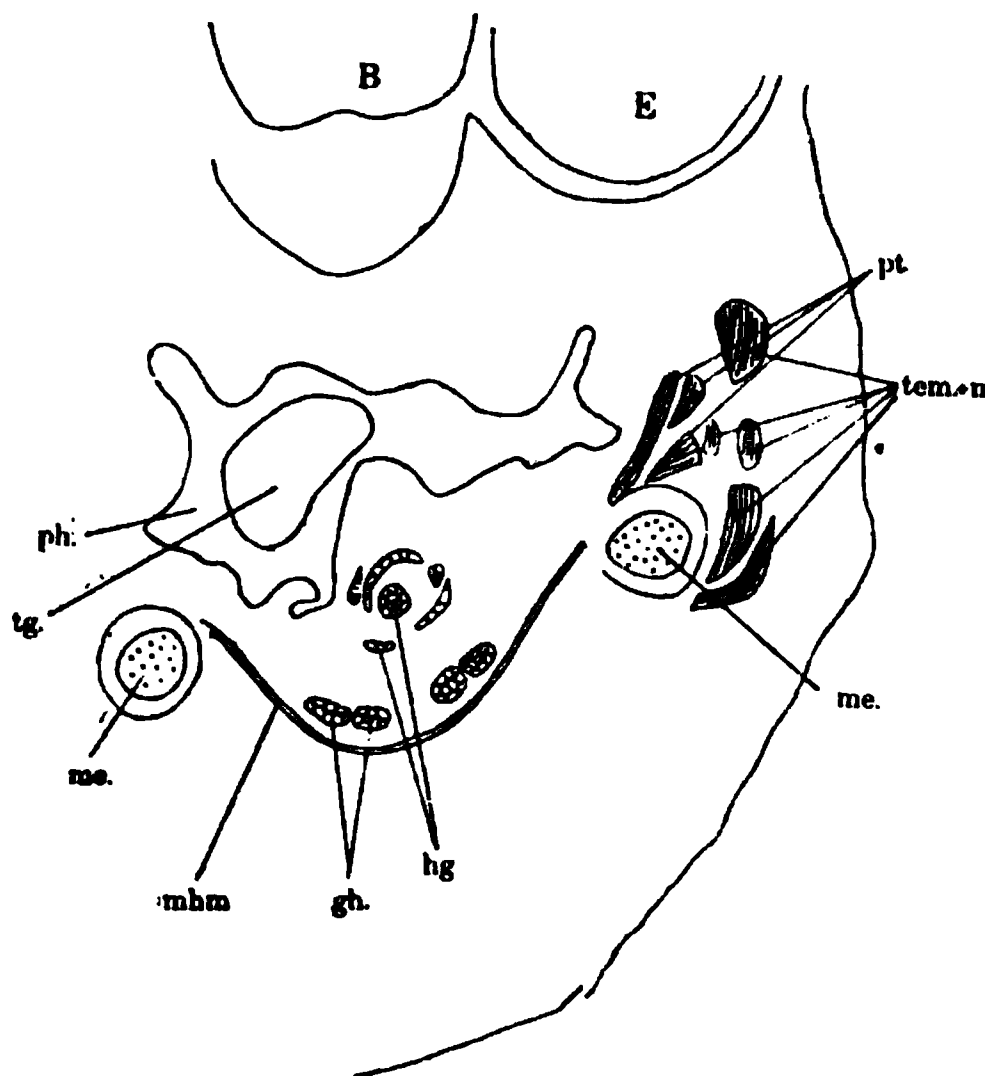


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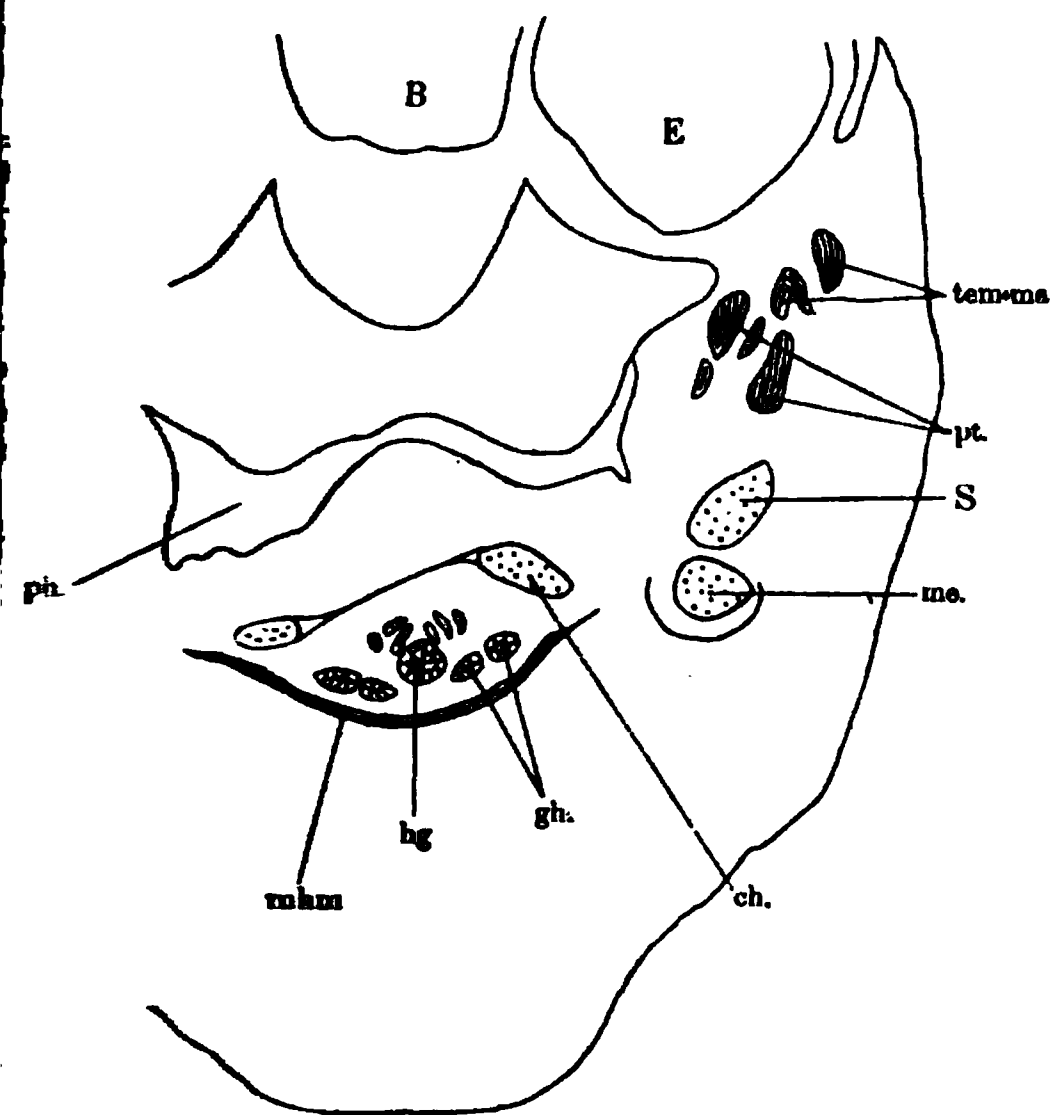


Fig. 43.

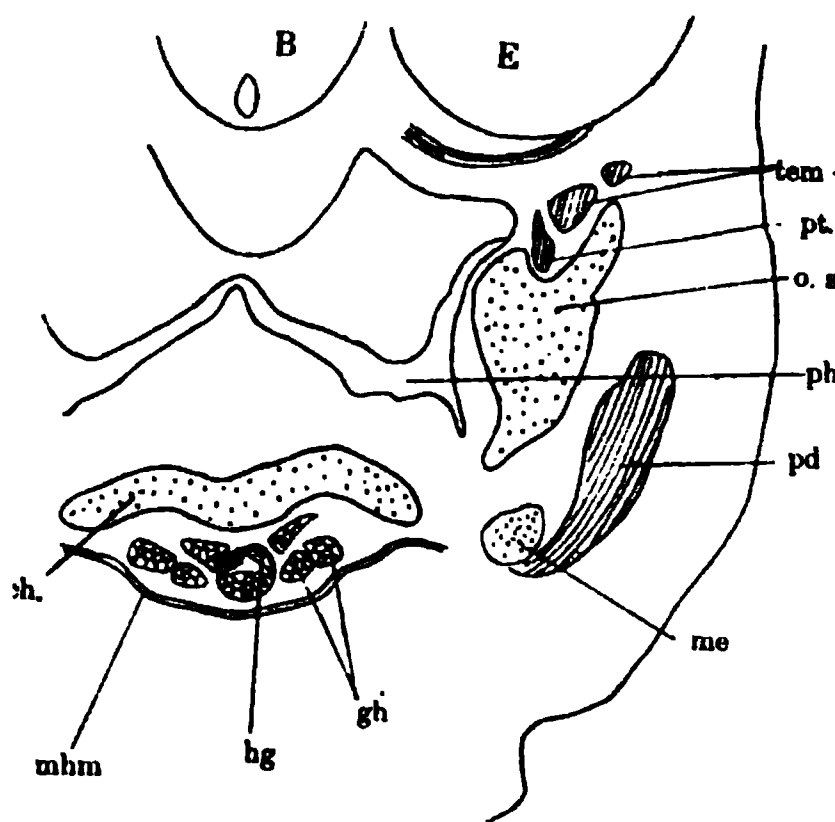


Fig. 44.





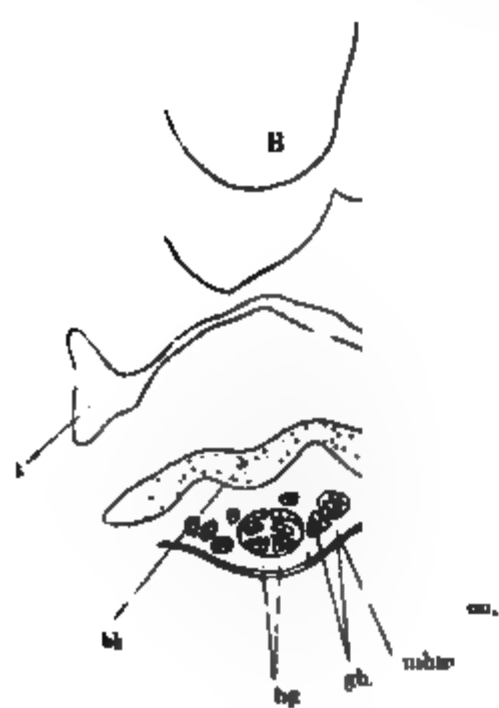


Fig. 45.

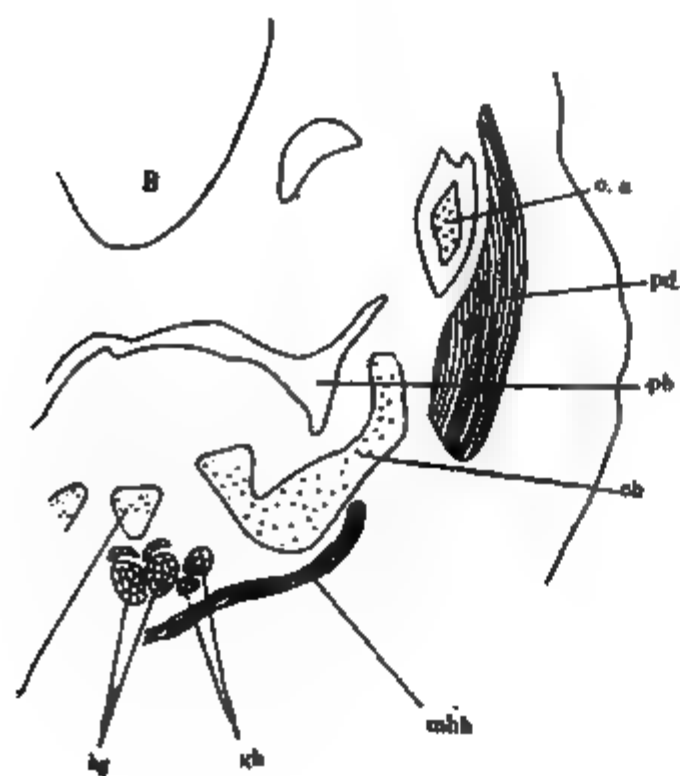


Fig. 46.

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ot, hy 1.  
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Fig. 49.

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Fig. 47.

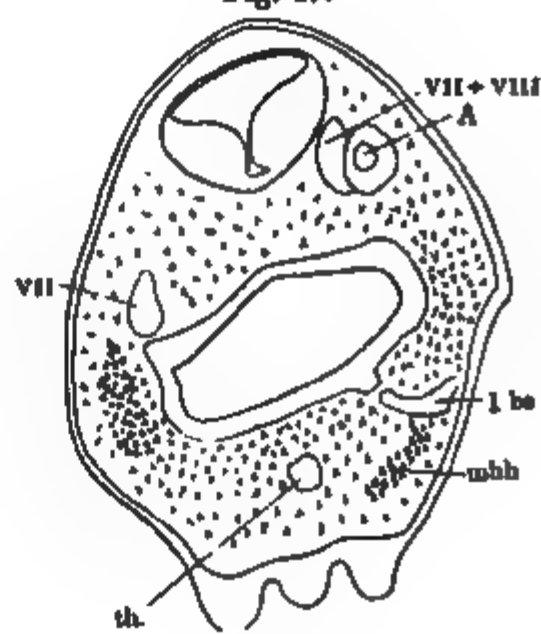


Fig. 48.

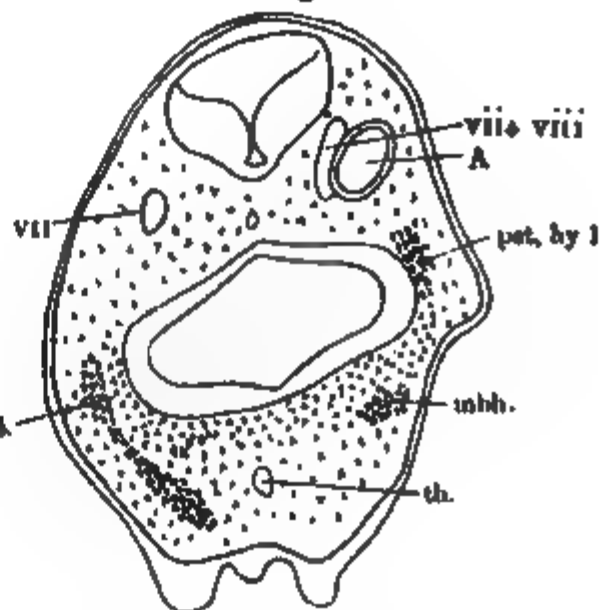


Fig. 50.

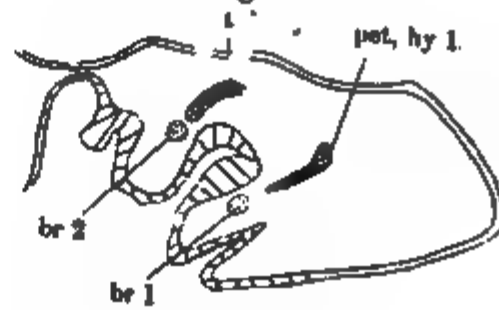


Fig. 51.



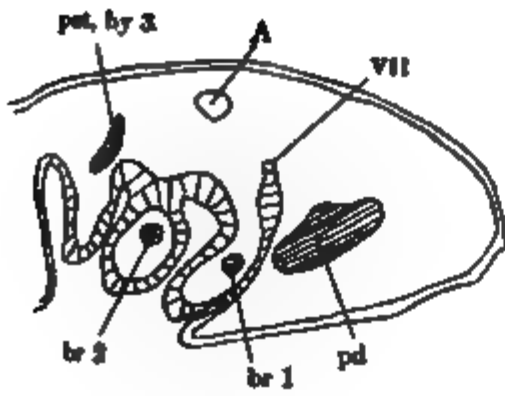


Fig. 52.

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br 2      br 1  
Fig. 53.

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shu.  
sh.  
gh.  
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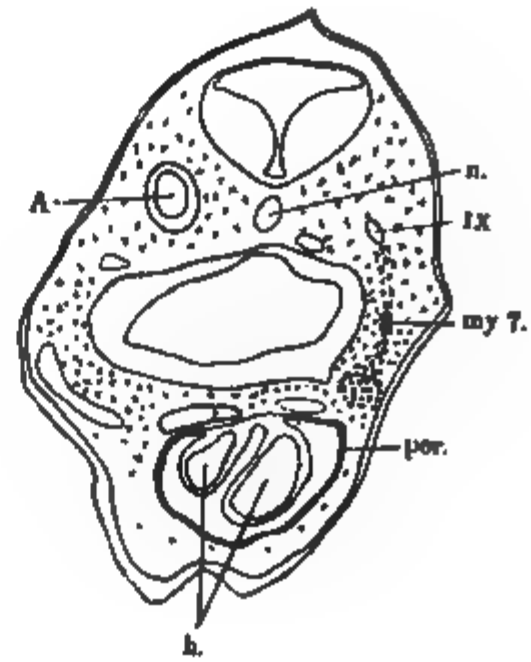


Fig. 55.

Fig. 54.

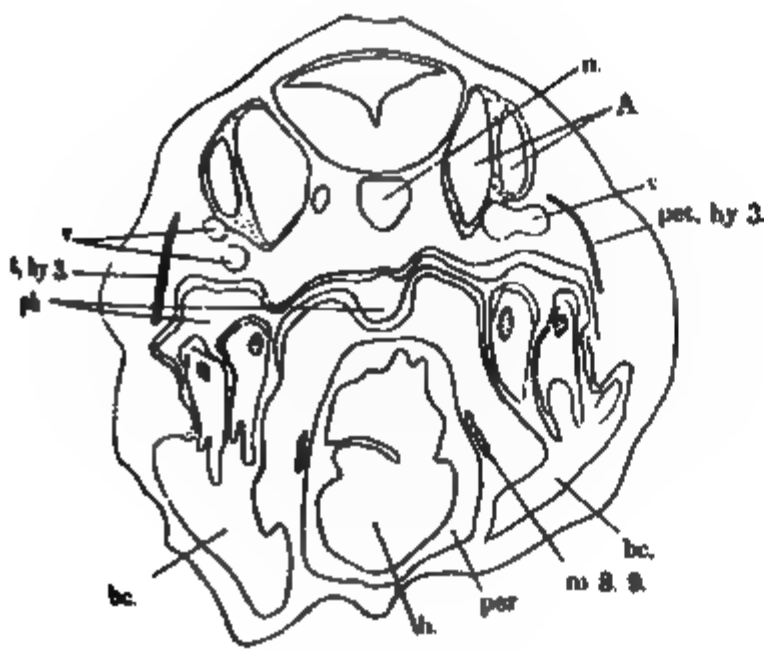


Fig. 57.

pet. hy 2

pet. hy 2

bc.  
gh.

Fig. 56.



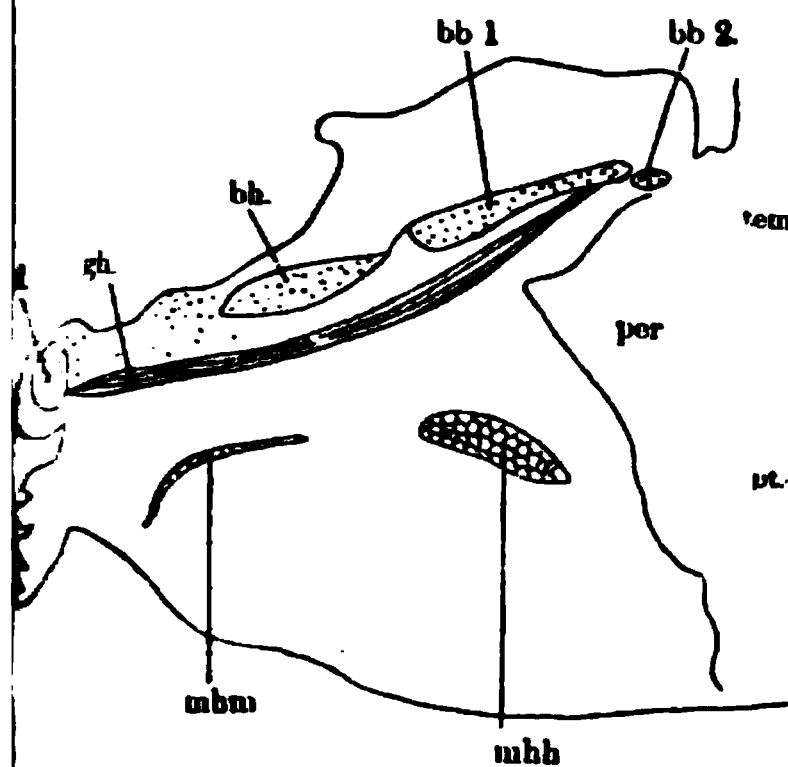


Fig. 58.

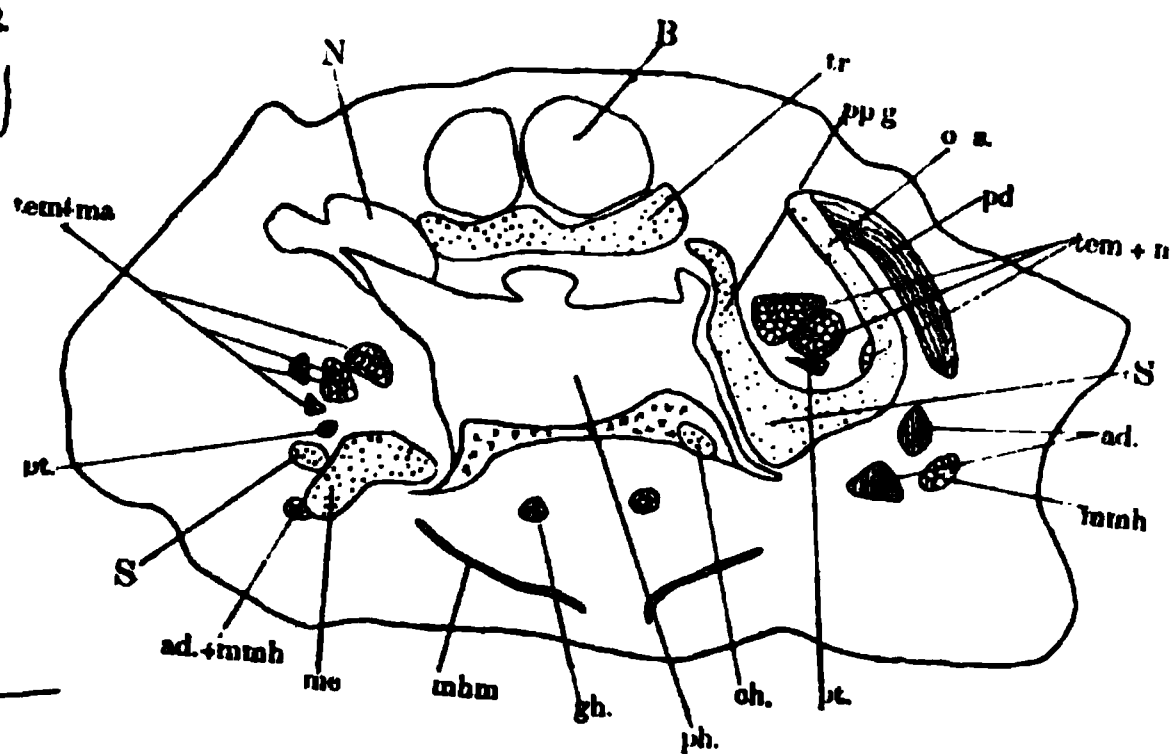


Fig. 59.

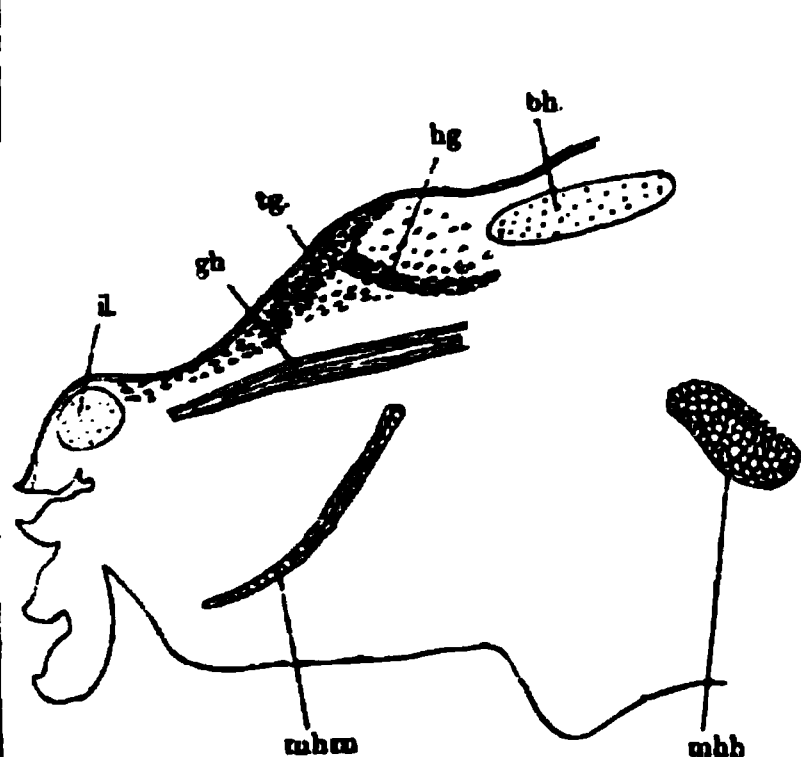


Fig. 60.

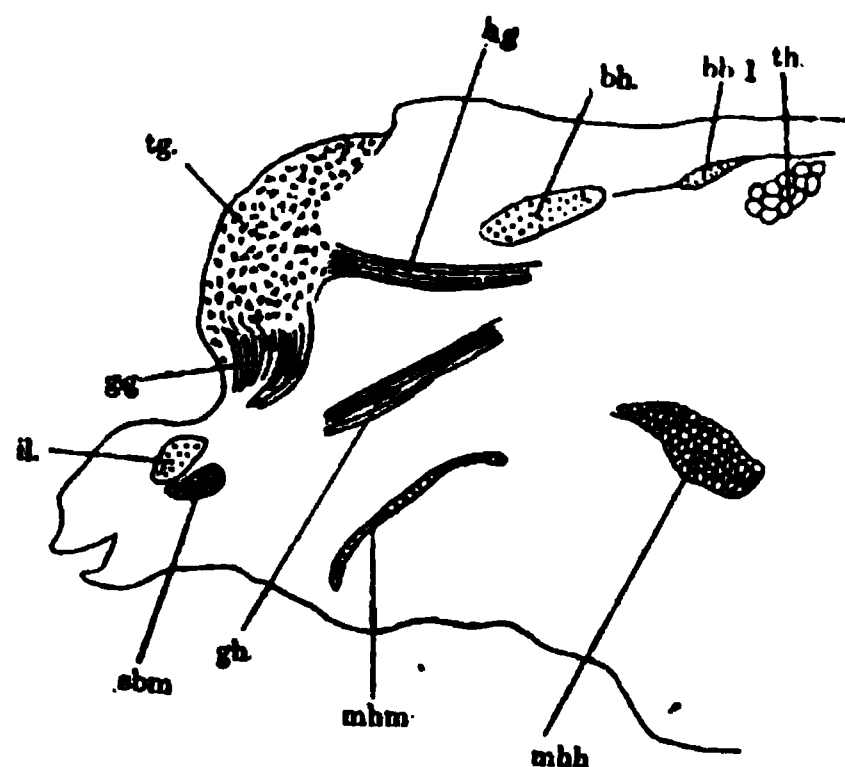


Fig. 62.

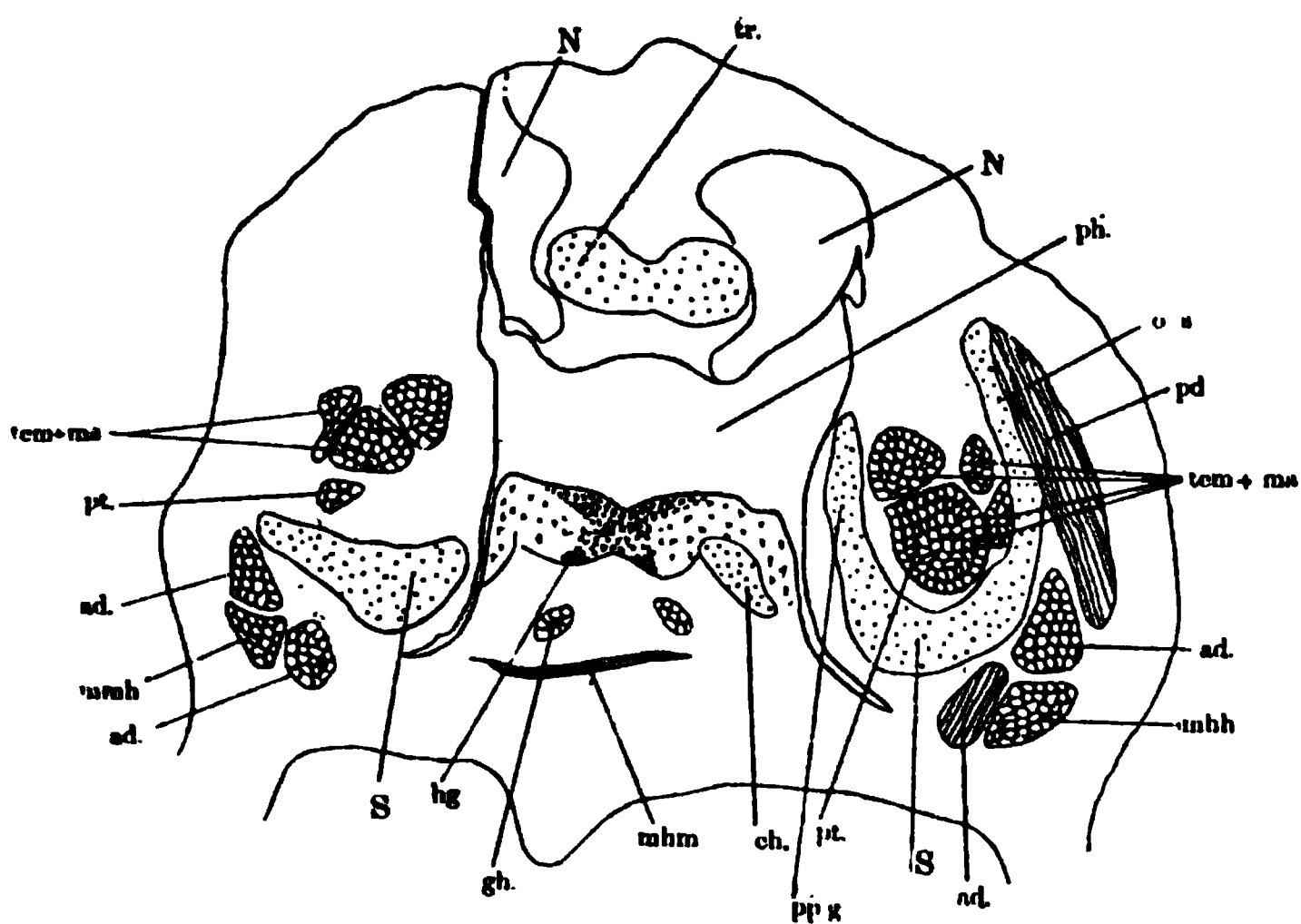


Fig. 61.



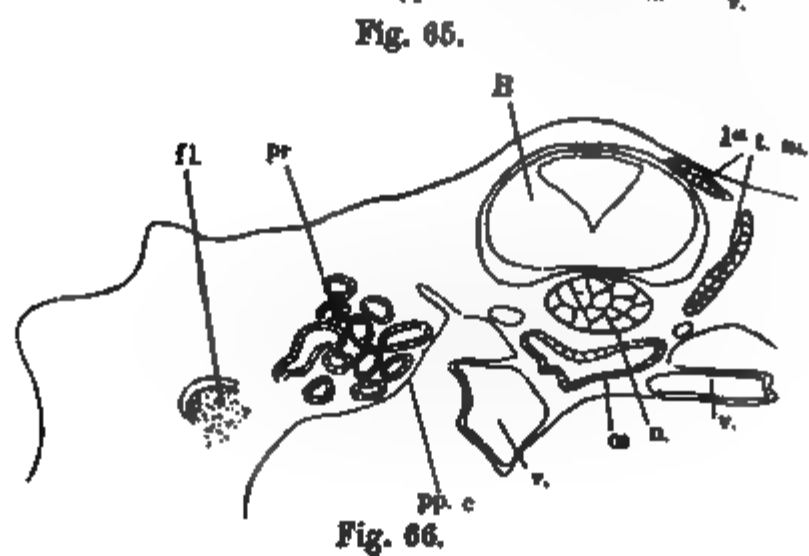
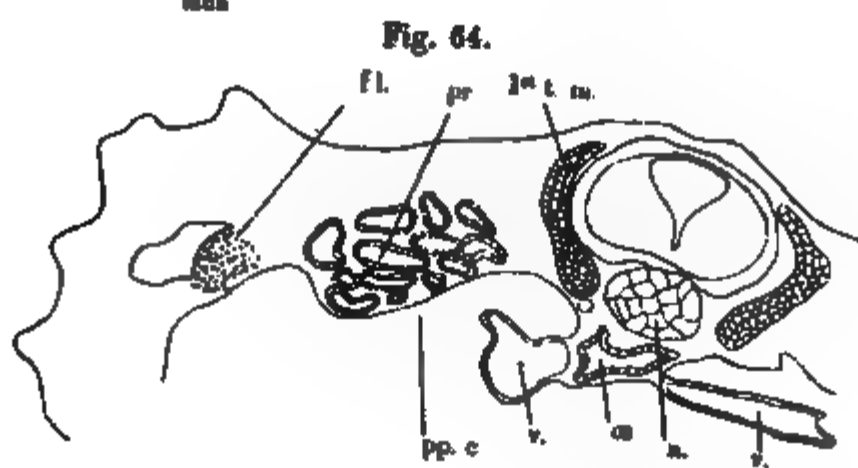
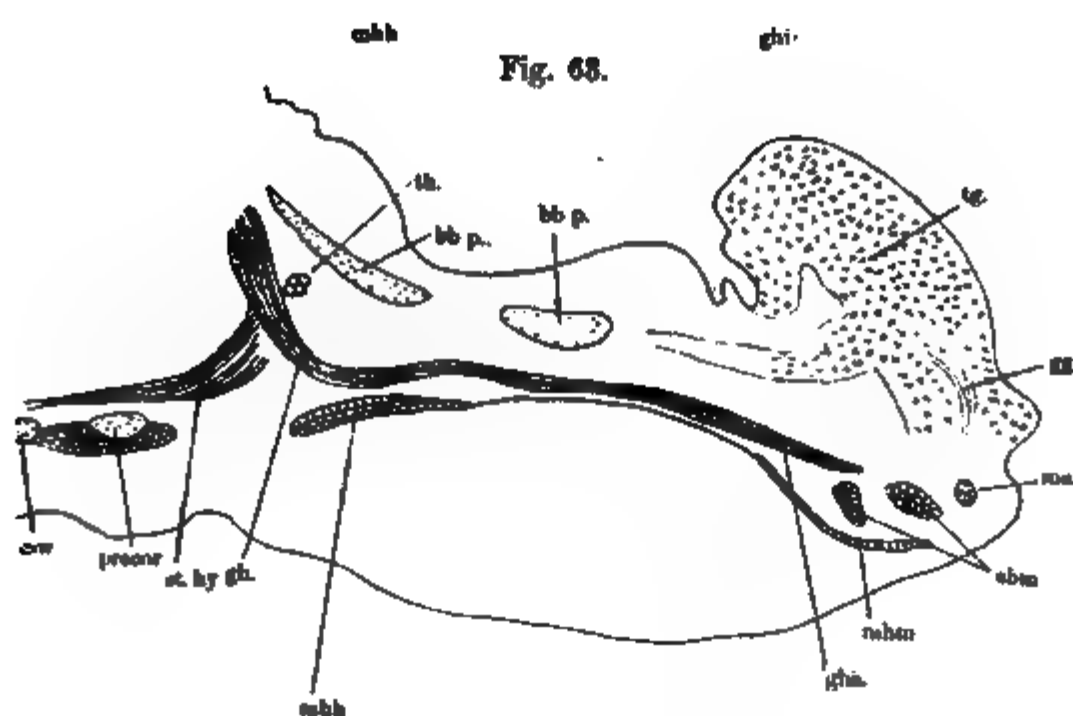


Fig. 66.





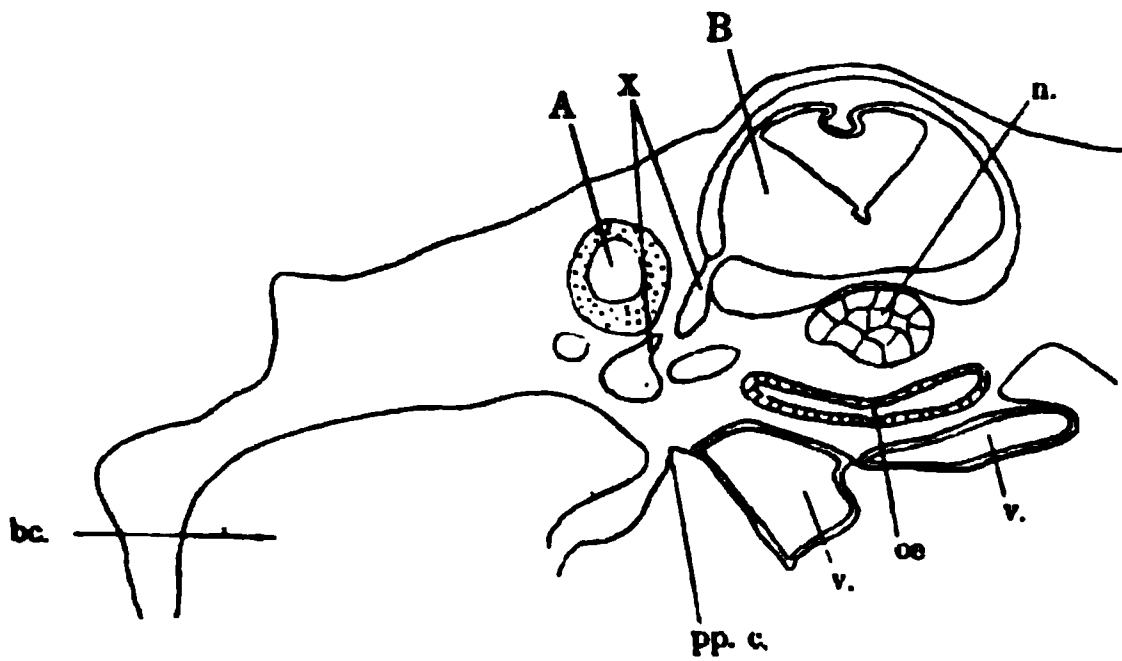


Fig. 67.

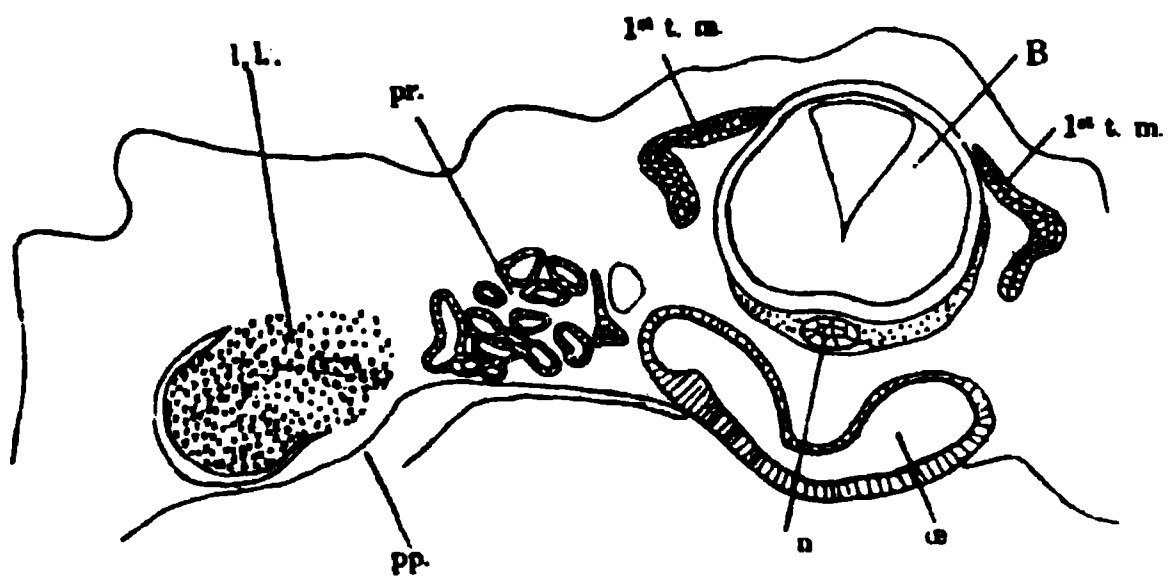


Fig. 68.

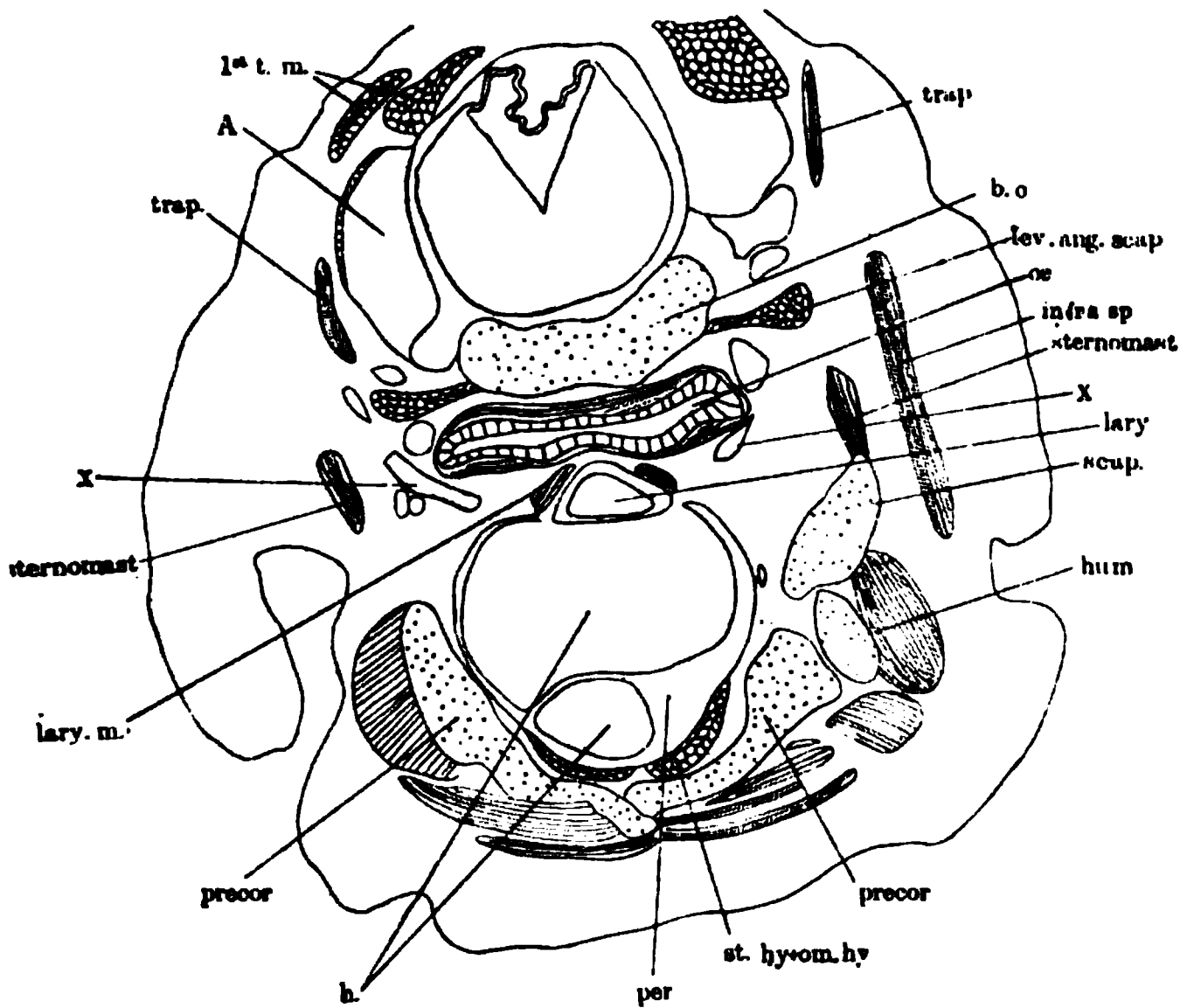
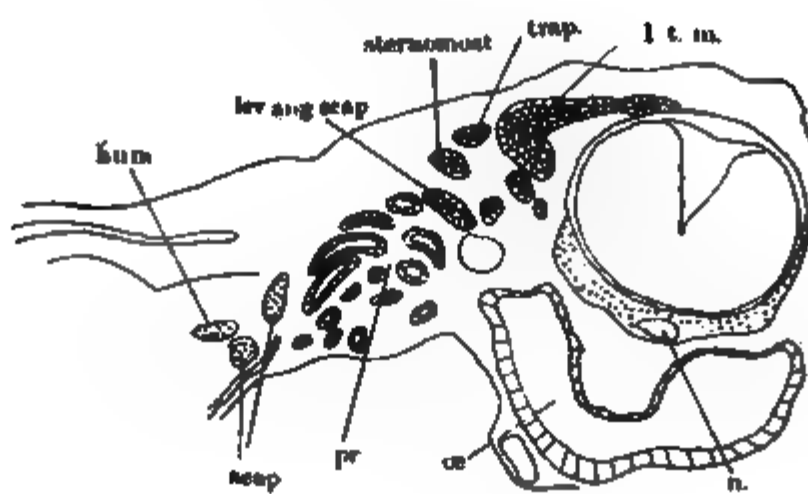


Fig. 71.





**Fig. 69.**

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**Fig. 70.**

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**Fig. 72.**



ON THE MEDULLATED FIBRES OF SOME OF THE CRANIAL NERVES, AND THE DEVELOPMENT OF CERTAIN MUSCLES OF THE HEAD. By F. H. EDGEWORTH, M.B. (Cantab.), B.Sc. (Lond.), *Assistant Physician to the Bristol Royal Infirmary.* (PLATES X.-XXII.).

THIS paper may conveniently be divided into the following sections:—i. Introduction; ii. Individual Cranial Nerves; iii. Classification of Muscular Branches; iv. Development of Certain Cranial Muscles; v. Classification of Cranial Motor Nuclei; vi. Collateral Evidence from Disease; vii. Sensory Branches; viii. General Conclusions.

i. INTRODUCTION.

The observations which are here described were begun some years ago, at the suggestion of Dr Gaskell, with the intention of investigating the sensory branches only of the cranial nerves in the dog. The investigation was extended to mixed and motor branches, and to the origin and development of some of the cranial muscles.

The paper may be considered, in so far as it contains new views, as a series of proposed amendments to Dr Gaskell's paper on the cranial nerves.<sup>1</sup>

The nerves are described more or less in order from before backwards, and subsequently the various motor and sensory fibres are separately discussed. One or two preliminary remarks are, however, needful. The medullated fibres in any nerve, or branch of a nerve, are said to vary in size up to a certain maximum diameter. By this is meant that fibres of all sizes occur from about  $1.5\ \mu$  in diameter up to the number given. It was not found possible to separate nerve fibres of similar sizes into groups, by reason of differing thickness of medullary sheath or size of axis-cylinder. Though a little variation exists, yet in general the thickness of the sheath, and

<sup>1</sup> *Jour. of Phys.*, vol. ix.

so the size of the axis-cylinder, was found to be very closely proportional to the diameter of the fibre. Hence, though Gaskell<sup>1</sup> has shown that conclusions as to the morphological position of the structures innervated can be drawn from the maximum diameter of the nerve fibres, and has correspondingly stated these only, yet in the following description the fibres are said to vary up to a certain diameter in each case.

Small differences in the maximum size of the fibres in any one nerve, cut close to its superficial origin from the brain, were found in specimens taken from different dogs. For instance, the maximum diameter of the fibres in the III nerve was found to vary between 16 and 17·6  $\mu$ ,<sup>2</sup> and in one or two instances was as low as 14·4  $\mu$ .

If sections of any one nerve were made at various distances from its origin, it was found that the maximum size of the fibres was somewhat less the more distal the section. For instance, the maximum diameter of the fibres in the ophthalmic branch of the V just beyond its exit from the Gasserian ganglion was found in one case to be 17·6  $\mu$ , whilst in the various branches no fibres of diameter greater than 16·8  $\mu$  were seen. Diminution in size from these causes takes place in different degrees in different animals; for instance, the maximum diameter of the fibres in the nerve to the crico-thyroid muscle, cut about  $\frac{1}{4}$  inch outside its entry into the muscle, was found in some cases to be as high as 12·8, in others as low as 9·6  $\mu$ .

In the following descriptions the average maximum diameter found in any nerve, or branch of a nerve, is recorded; subsequently, in discussing the various motor and sensory fibres, consideration is given to the question whether the extremes of variation invalidate the generalisations.

The nerves were stained in osmic acid, imbedded in paraffin, and examined in cross section, and measurements were taken only in cases where no puckering or shrinking of the nerve fibres existed.

<sup>1</sup> *Loc. cit.*

<sup>2</sup> The maximum size of the fibres found in the III and certain other nerves is stated by Gaskell to be 18  $\mu$ . Possibly owing to the class of dogs dissected—mongrel English terriers—I have not come across quite so high a figure; the difference, however, is unessential.

## ii. THE CRANIAL NERVES.

The III, IV, and VI nerves consist each of medullated fibres, varying in diameter up to  $16\ \mu$ . Although the majority of the fine fibres (*i.e.*, fibres under  $4\ \mu$  in diameter) in the III pass to the ciliary ganglion, yet not all do so; thus each external ocular muscle receives small as well as larger medullated fibres.

The branch of the VI to the retractor bulbi contains fibres up to the same maximum diameter as occur in the continued trunk of the VI to the external rectus.

Each of the oculo-motor nerves receives one or more fine filaments from the carotid plexus, consisting mainly of grey fibres, together with one or two medullated fibres up to  $6.4\ \mu$  in diameter. Each also receives a fine branch from the ophthalmic division of the V, consisting of grey fibres and a few fine medullated fibres up to  $5.6\ \mu$  in diameter. As all the grey fibres in the ophthalmic division of the V come from the carotid plexus, and none from the Gasserian ganglion, the grey fibres in these fine branches to the oculo-motor nerves must eventually have the same origin.

V.—If serial sections be made through the roots of the trigeminal nerve, it can be seen that the first two divisions and the sensory branches of the third division (with exception of the mylo-hyoid) do not receive any fibres from the motor root.

These sensory branches can be divided into two classes by the maximum size of their medullated fibres.

Grey fibres and medullated fibres up to  $16\ \mu$  in diameter are found in the long ciliary, ethmoidal, and infratrochlear branches of the ophthalmic division; in the lacrymal, subcutaneous malar, infraorbital (both dental and skin branches), palatinus major, and nasalis posterior, from the superior maxillary division; and in the auriculo-temporal, buccal, terminal branches (*i.e.*, to skin) of the mylo-hyoid, mental and dental branches of inferior dental, from the inferior maxillary division.

Grey fibres and medullated fibres up to  $11.2\ \mu$  in diameter occur in the palatinus minor from the superior maxillary division; in the lingual, orbital gland branches of the buccal

and parotid gland branches of the auriculo-temporal, from the inferior maxillary division.

The Gasserian ganglion does not give rise to any grey fibres, which come, together with a few smallish fibres, from the carotid plexus. The nasalis posterior, palatinus major and minor also receive grey fibres from or through the spheno-palatine ganglion; and the sensory branches of the inferior maxillary division, some grey ones from or through the otic ganglion.

The branches of the V which pass to muscles can also be divided into two sets by the maximum sizes of their medullated fibres. Grey fibres and medullated fibres up to a maximum diameter of  $16\ \mu$  occur in the branches passing to the temporal, masseter, pterygoids, and anterior portion of the digastric muscles.<sup>1</sup>

Grey fibres and medullated fibres up to a maximum diameter of  $11.2\ \mu$  occur in the nerves to the tensor tympani, tensor veli palatini, and mylo-hyoid muscles.

The grey fibres in the motor branches come from the carotid plexus.

VII *nerve*.—The roots of the facial nerve are described by Gaskell<sup>2</sup> as consisting of a 'large-fibred' portion and a 'small-fibred' portion (n. intermedius). The large-fibred portion consists of "a few fibres of the smallest size, but is mostly composed of the motor fibres of the facial muscles, which are very uniform in size, and measure about  $10.8\ \mu$ . In addition to these, there are a very large quantity of fibres which measure between 7 and  $8\ \mu$ ." The n. intermedius "is essentially a small-fibred formation, with a few much larger fibres."

In the dogs examined, the fibres of the facial nerve were found to be of all diameters up to  $11.2\ \mu$ ; there were also to be seen a few fibres of larger size up to  $16\ \mu$  in diameter. Some of these larger fibres were aggregated together at that part of the facial root most remote from the n. intermedius, but a few were also seen throughout it. The larger fibres of the n. intermedius or sensory root of the facial were found to be of all diameters up to  $11.2\ \mu$ . With one exception, all the branches

<sup>1</sup> The anterior and posterior digastric form a muscle with one belly in the dog. *Vide* Ellenberger and Baum, *Anatomie des Hundes*.

<sup>2</sup> *Loc. cit.*



of the facial distal to its exit from the stylo-mastoid foramen, and also the branch to the stapedius muscle, were found to consist of grey fibres and medullated fibres up to  $11.2\ \mu$  in diameter. The exception is that branch<sup>1</sup> of the facial which divides into two to supply the posterior digastric and stylo-hyoid muscles. This branch, and each of its two divisions, were found to consist of grey fibres and medullated fibres, of all diameters up to  $16\ \mu$ . The largest fibres it contains can, as described by Gaskell, be distinguished in the facial root, traced down laterally to the geniculate ganglion, and seen to separate gradually out from the facial trunk to help to form the branch in question.

The chorda tympani consists of medullated fibres of various diameters up to  $11.2\ \mu$ ; of these the small fibres are far more numerous.<sup>2</sup>

The great superficial petrosal consists of grey fibres and medullated fibres up to  $11.2\ \mu$  in diameter; it is a very small nerve, and contains but few fibres.

No fibres can be traced, by microscopical examination only, directly from the n. intermedius into the great superficial petrosal, or from the great superficial into the nerve which, issuing from the geniculate ganglion, runs down alongside the facial, and which consists of grey fibres and medullated ones, of all diameters up to  $11.2$ . From examination of serial sections across the facial trunk in the bone, it appears that of the nerve fibres issuing from the geniculate ganglion, some of the medullated ones separate off to form the chorda tympani, though a large number of the grey ones join the motor part of the facial, and become mingled with them. (This is confirmed by the experiment mentioned later.) Vulpian<sup>3</sup> stated that if the root of the facial, including the n. intermedius, be cut through in the dog, the chorda, with exception of a very few fibres, five to ten at most, remains intact, whereas the facial fibres degenerate. It is not stated, however, whether any undegenerated fibres were finally left in the facial trunk. The further experiments of Vulpian are to the effect that intra-cranial section of the V

<sup>1</sup> This is the branch described by Gaskell as leaving the facial trunk just before its exit from the bone, the distribution of which, however, he did not trace.

<sup>2</sup> Vide Langley, *Jour. of Phys.*, vol. xi.

<sup>3</sup> *Gaz. méd. de Paris*, 1878.

in rabbits, the VII being uninjured, caused almost total degeneration of the chorda.

These experiments do not harmonise with the fact stated above, that the number of medullated fibres in the chorda is much greater than in the great superficial petrosal, and are in disaccord with the embryological researches of Dixon,<sup>1</sup> who has shown that the great superficial petrosal grows out from the geniculate ganglion.

All the branches of the facial, with exception of the chorda, contain grey fibres, whilst the root of the nerve does not. It follows that they come into the nerve *via* the great superficial petrosal. As the facial is traced outwards in the bone, the grey fibres are seen to increase markedly in numbers, probably by division.

IX, X, and XI nerves.—The roots of the IX, X, and medullary part of the XI consist of medullated fibres of various sizes up to  $11.2\ \mu$  in diameter. One of the upper rootlets of the X contains larger fibres up to  $16\ \mu$  in diameter. These larger fibres, together with a few grey ones, pass off just below the jugular ganglion as the auricular branch of the vagus, and below that point no medullated fibres of diameter greater than  $11.2\ \mu$  are found in the IX, X, and medullary XI nerves.

It is stated by Gaskell<sup>2</sup> that the small fibres of the spinal part of the XI join the vagus below the jugular ganglion.

The roots of the spinal portion of the XI contain medullated fibres of all sizes up to  $16\ \mu$  in diameter. The external branch of the XI, which is derived solely from the spinal portion of the XI, consists of grey fibres and medullated fibres, of all diameters up to  $16\ \mu$ . The grey fibres can be traced into the external branch from the superior cervical ganglion. Examination of serial sections taken through the X and XI shows that all the fibres of the spinal portion of the XI pass off into its external branch, and that none join the X, whereas all the fibres of the medullary portion of the XI join the X below the jugular ganglion. Spencer<sup>3</sup> also states that in the monkey and man the spinal roots of the XI form the external branch only, and the medullary roots join the X.

<sup>1</sup> *Trans. Roy. Dub. Soc.*, series ii. vol. iv.

<sup>2</sup> *Loc. cit.*

<sup>3</sup> *Lancet*, 1895.

The spinal accessory proper (spinal roots of XI) is then distinct, both in origin and distribution, from the vago-accessory (medullary roots of XI).

The recurrent laryngeal consists of very few grey fibres and medullary fibres, up to  $11.2\ \mu$  in diameter. A septum of perineurium separates the fibres into two groups—the abductors and adductors of the vocal cords.<sup>1</sup> No histological distinction can be drawn between the fibres on either side the septum; there are no visible differences in the diameters of the axis-cylinders, or in the thicknesses of the medullary sheaths, to which the differences in vulnerability<sup>2</sup> between the abductor and adductor fibres might have been attributed. It would appear, then, that the differences in vulnerability between the abductor and the adductor ganglion cells in the medulla<sup>3</sup> extend to, and are shared by, their axis-cylinder processes.

The communicating branch between the superior and inferior laryngeal, which Howell and Huber<sup>4</sup> have shown to be a branch of the former nerve, and sensory in function, consists of a few grey fibres and medullated ones, up to  $11.2\ \mu$  in diameter.<sup>5</sup> The terminal portion of the superior laryngeal, after it has given off its communicating branch, has the same structure as its branch. The terminal portion of the lingual branch of the IX, and also its branch to the keratoglossus, and the pharyngeal branches of the IX and X, consist of grey fibres and medullated fibres up to  $11.2\ \mu$ .

The cardiac branches of the vago-sympathetic,<sup>6</sup> the cardiac branches of the recurrent laryngeal, the pulmonary nerves, and the vagus beyond the pulmonary have the same structure. The number of grey fibres in these nerves varies: the vagus beyond the pulmonary consists very largely of them, the cardiac nerves contain relatively fewer, and the pulmonary a still smaller number. The number of larger medullated fibres is very great in the pulmonary, small in the cardiac nerves, and least in the

<sup>1</sup> Risien Russell, *Proc. Roy. Soc.*, 1892.

<sup>2</sup> Semon and Horsley, *Phil. Trans. Roy. Soc.*, 1890.

<sup>3</sup> Semon, *Brain*, 1892.

<sup>4</sup> *Jour. of Phys.*, vol. xii.

<sup>5</sup> The contrast between the communicans and the recurrent laryngeal, which lie alongside each other below the larynx, in respect to the large number of small medullated fibres in the former and their fewness in the latter, is very striking.

<sup>6</sup> For anatomy, *vide* Lim Boon Keng, *Jour. of Phys.*, vol. xiv.

vagus beyond the pulmonary. To ascertain approximately what proportion of the medullated fibres in the pulmonary and cardiac nerves come from the vagus and sympathetic (the latter *via* the annulus of Vieussens), an inch of the vagus was cut out in the neck of a dog, and the nerves examined five weeks subsequently. It was found that the pulmonary and cardiac nerves had lost the greater portion of their medullated fibres, but that some were intact in each branch examined.

One or two conclusions result from a comparison of the structure of the various branches of the IX, X, and medullary XI.

Motor fibres of all sizes up to  $11.2\ \mu$  are found in the recurrent laryngeal, crico-thyroid branch of superior laryngeal, in the superior and inferior pharyngeal, in the pharyngeal branch of the IX, and in the stylo-pharyngeus branch of the IX.

It is not possible, by microscopical examination simply, to determine their exact origin in the roots of the IX, X, and medullary XI, but it has been shown by Horsley and Beever,<sup>1</sup> and by Rethi,<sup>2</sup> that the stylo-pharyngeus is innervated by the IX, and by Rethi that the palato-glossus, palato-pharyngeus, constrictores pharyngei, levator veli palatini, and azygos uvulae are innervated by the X, whilst the laryngeal muscles are supplied from the medullary XI. And it is stated by Spencer<sup>3</sup> that the crico-thyroid is innervated by the IX.

Sensory medullated fibres, up to  $11.2\ \mu$  in diameter, are found in the lingual branch of the IX, in the superior laryngeal and its communicating branch, and in branches where (from the character of the muscles supplied) it is probable that similar fibres are also sensory in function, *i.e.*, in the cardiac and pulmonary branches, and in the vagus below the origin of the pulmonary nerves. Probably, also, some of the medullated fibres in the pharyngeal IX, in the superior and inferior pharyngeal nerves, are also sensory.

As to the origin of these sensory fibres, it has been shown by Gaskell that the medullary XI passes by the g. jugulare of the X, so that it appears probable that they come from the IX and

<sup>1</sup> Horsley and Beever, *Proc. Roy. Soc.*, 1888.

<sup>2</sup> *Sitzungsber. der Kais. Akad. d. Wissenschaft*, Wien, 1892 and 1893.

<sup>3</sup> *Lancet*, 1895, and literature referred to by him.

X roots, with posterior root ganglia in the jugular ganglia of these nerves.

It is to be remarked that no histological distinction can be drawn between the medullated fibres in the superior laryngeal—which, as regards respiration, conduct only expiratory stimuli—and those in the pulmonary nerves—which conduct both expiratory and inspiratory stimuli, nor between these fibres and those found in the lingual branch of the IX, and in the cardiac nerves.

It follows that there are no fibres of specialised diameter or sheath-thickness concerned in carrying expiratory or inspiratory stimuli, or in conveying afferent cardiac impulses, or those impulses which pass up the lingual branch of the IX. The specialisation of these fibres, from a functional point of view, is not dependent on, or has not led to, histological differentiation, but must be due either to their peripheral or central terminations, or to both of these factors.

One other point may be noticed. From the results of clinical examination, it is held<sup>1</sup> that taste impulses passing up the lingual branch of the IX do not reach the central nervous system by the root of the IX, but turn aside through the n. tympanicus to reach the V.

The n. tympanicus, which Dixon<sup>2</sup> has shown to grow up from the IX, consists of grey fibres and medullated ones up to  $11.2\ \mu$  in diameter, but the number of medullated fibres is very few. The IX also gives off the branches described by Langley<sup>3</sup> to the tympanic plexus.

In the case, then, both of the chorda and lingual IX, the number of medullated fibres which might possibly have come from the V forms a very small proportion of those which they contain.

XII.—The roots of the XII were described by Gaskell<sup>4</sup> as consisting of fine fibres, and of fibres of from  $7.2$  to  $10.8\ \mu$ . In the dogs examined, it was found that whereas the upper rootlets of the hypoglossal contain medullated fibres of all sizes up to  $11.2\ \mu$ , in the lower rootlets the maximum diameter was as great as  $16\ \mu$ .

<sup>1</sup> *Vide Gowers' Dis. of Nerv. System*, vol. ii.

<sup>2</sup> *Proc. Phys. Soc.*, 1893.

<sup>3</sup> *Loc. cit.*

<sup>4</sup> *Loc. cit.*

The rootlets converge to form the trunk of the nerve, throughout which the largest fibres are uniformly scattered. The nerve also receives the ganglionated root of Froriep and Gaskell, which consists of medullated fibres up to  $11\cdot2\ \mu$  in diameter. It receives extra-cranially one or two fine branches from the vagus and pharyngeal plexus, consisting of medullated fibres up to  $11\cdot2\ \mu$  in diameter, and a largish branch from the sympathetic, consisting mostly of grey fibres, with a few small medullated ones. It does not receive any branch from the 1st cervical.

The branches of distribution may be divided into two sets by the maximum diameter of the medullated fibres. In the descendens hypoglossi (and each of its branches to the thyro-hyoid, and anterior portions of the sterno-hyoid and sterno-thyroid), and in the genio-hyoid, the maximum diameter is  $16\ \mu$ , whilst in all the other branches the maximum diameter is  $11\cdot2\ m$ . All the branches contain grey fibres, which have come from the sympathetic.

In the dog, then, the XII innervates the tongue muscles, the genio-hyoid, thyro-hyoid, and anterior portions of the sterno-hyoid and sterno-thyroid; whilst the communicans hypoglossi, which sends a small branch to the descendens and innervates the lower part of the sterno-hyoid and sterno-thyroid (the omohyoid being absent in the dog), comes from the first cervical nerve.<sup>1</sup>

On comparing this with the experimental investigations of Horsley and Beevor<sup>2</sup> and of Risien Russell<sup>3</sup> in the monkey, a difference is seen to exist. In both animals the genio-hyoid is innervated by the hypo-glossal roots; but whereas in the monkey the descendens hypoglossi comes from the first and the communicans from the second cervical root, in the dog the descendens is a part of the hypo-glossal, and the communicans comes from the first cervical.

The hyoid depressors are, then, post-fixed<sup>4</sup> in the monkey as compared with the dog.

The anatomy of the nerves in man suggests that the condition is like that in the monkey.

<sup>1</sup> *Vide* Ellenberger and Baum, *Anatomie des Hundes*.

<sup>2</sup> *Proc. Roy. Soc.*, 1888, and *Brit. Med. Jour.*, 1888.

<sup>3</sup> *Brain*, 1887.

<sup>4</sup> Using Sherrington's nomenclature.

*Medullated fibres of sympathetic origin.*—Before any attempt is made to classify the medullated fibres in the various branches of the cranial nerves, the medullated fibres which have entered these branches from the sympathetic must first be considered. They are, as stated above in describing individual nerves, exceedingly few in number, and are mostly under  $4\ \mu$  in diameter, and the largest seen had a diameter of only  $6.4\ \mu$ . The general statements made below will therefore not be affected by the existence of these scanty medullated fibres of sympathetic origin.

### iii. CLASSIFICATION OF MUSCULAR BRANCHES.

If the diameters of the fibres in the branches of the cranial nerves passing to muscles be compared with one another, it is seen that the nerve fibres may be separated into two divisions by their maximum sizes.

(a) Nerve fibres of all sizes up to  $16\ \mu$  in diameter are found in the III (external ocular muscles), IV (superior oblique), VI (external rectus and retractor oculi), V (temporal, pterygoids, masseter, and anterior digastric), VII (posterior digastric and stylo-hyoid), XII (genio-hyoid, thyro-hyoid, and anterior portions of sterno-hyoid and sterno-thyroid), and XI spinal (sternomastoid and trapezius).

( $\beta$ ) Nerve fibres of all sizes up to  $11.2\ \mu$  in diameter are found in the V (mylo-hyoid, tensor tympani, and tensor veli palatini), VII (facial muscles), IX (stylo-pharyngeus), X (palatoglossus, palato-pharyngeus, constrictores pharyngei, azygos uvulæ, and levator veli palatini), XI (medullary laryngeal muscles), and XII (genio-glossus, hyo-glossus, and intrinsic tongue muscles).

As regards variation of maximum diameter in different animals, it was found that the maximum diameter of the fibres placed in the first division might be as high as  $17.6\ \mu$  or as low as  $14.4\ \mu$ , whereas that of the fibres in the second division varied between  $12.8\ \mu$  and  $9.6\ \mu$ . The maximum diameters of the two classes, then, do not overlap, but are separate and distinct.

Before the import of the existence of these two classes of cranial nerves can be discussed, consideration must be given to



the question whether all the fibres in these branches are motor (or at any rate direct) fibres, or whether some of the fibres in at least some of the branches may not be root ganglion fibres.

The first group of fibres in which the maximum diameter is as great as  $16\ \mu$  may be taken first. It is obvious that the III (external ocular muscles), IV, VI, and XI (spinal) have no posterior root ganglia. All the medullated fibres in them come directly from the central nervous system. This suggested that the other muscles of this group were also devoid of root ganglion fibres. An attempt was made to decide the question by inspection of serial sections through the roots of the nerves. In the case of the VII and XII it was not found possible to come to any decision, the fibres become so inextricably mingled. In the V, however, it was quite easy to see that the branches to the temporal, masseter, and pterygoid muscles come exclusively from the motor root, and receive no fibres from the sensory root of the V.<sup>1</sup> The branch to the anterior digastric separates from the mylo-hyoid nerve so low down that it might or might not (as far as microscopical examination went) have fibres in it coming from the sensory root.

Further, Dr Aldren Turner was good enough to divide the VII nerve intra-cranially (*i.e.*, above the geniculate ganglion) in a rhesus monkey. The branches were examined after an interval of three weeks. Inspection of the nerve fibres of the facial nerve on the uncut side showed that the maximum diameter of those passing to the posterior digastric and stylo-hyoid muscles was  $14.4\ \mu$ , whilst that of the nerve fibres in the other muscular branches of the facial was  $12.8\ \mu$ . This is a difference similar to that which occurs in the dog. On the cut side it was found that in the branch of the facial to the posterior digastric and stylo-hyoid muscles, all the medullated fibres had disappeared with exception of three only, all of which were under  $4\ \mu$  in diameter. On the other hand, in the continued trunk of the facial, after it had given off this branch, although a very large number of the medullated fibres had gone, many (? a third of the original number) persisted: these were of all diameters up to  $11.2\ \mu$  as a maximum. Insomuch as it is probable that the

<sup>1</sup> It was subsequently ascertained, from Dixon's paper (*loc. cit.*), that this fact had previously been stated by His.



three small fibres in the posterior digastric and stylo-hyoid branch come into the facial from without, possibly from the sympathetic, *via* the great superficial petrosal, it is concluded that whereas these muscles have no posterior root ganglion fibres passing to them, the other muscles innervated by the facial nerve receive not only motor fibres, but also many muscle-sensory fibres, having their posterior root ganglion cells in the geniculate ganglion.

In regard to the XII nerve, it is stated by Sherrington<sup>1</sup> that in an amyelous human foetus, in which "there existed not a single motor (ventral) spinal nerve root in any segment," "the hypo-glossal trunk reaches the tongue, and gives off a large leash of lingual twigs, as well as its usual branches to styloglossus, hyoglossus, genio-hyoideus, genio-hyo-glossus, and thyro-hyoideus. It gives off n. descendens noni as usual. Tracing the normal-looking nerve trunk backward, however, it seems to be almost exclusively formed by a branch from the 2nd cervical ganglion and another from the vagus below the vagus ganglion. I say almost, because a filament of it seems to be traceable to the base of the skull posterior to the vagus exit, and I then lose it." From this it appears probable that in the dog the muscles innervated by the XII and placed in the first division receive muscle-sensory as well as motor nerve-fibres.

Of the first group of muscles, then, it may be said that they receive no muscle-sensory nerves. To this statement the anterior digastric (V) is a doubtful, and the genio-hyoid, thyro-hyoid, and anterior portion of the sterno-hyoid and sterno-thyroid (XII) a positive, exception. On the other hand, the evidence as yet available points to the view that the muscles of the second group receive muscle-sensory fibres of all sizes up to a maximum diameter little short of that of their motor fibres. The above-described experiment gives positive evidence in the case of the facial nerve; and Sherrington states that in the above-mentioned foetus the branches of the vagus, including the recurrent laryngeal, the glosso-pharyngeal, and the V, were easily found, and, as above mentioned, that the lingual twigs of the XII were present.

The cranial motor nerve-fibres were divided by Gaskell<sup>2</sup> into

<sup>1</sup> *Jour. of Phys.*, vol. xii.

<sup>2</sup> *Loc. cit*

two groups,—‘somatic,’ supplying the muscles developed in the dorsal portions, and ‘non-ganglionated splanchnic,’ supplying the muscles developed in the ventral portions of the head somites. The III, IV, VI, and XII were included in the first, the V, VII, IX, X, XI (spinal and medullary) in the second division. This suggests that the muscles placed in the first division made above are somatic, and those in the second splanchnic in origin. This hypothesis is obviously a repetition of Gaskell’s classification in regard to the III, IV, VI, V (mylohyoid, tensor tympani, and tensor veli palatini), VII (facial muscles), IX, X, XI (medullary), XII (genio-hyoid, thyro-hyoid, and anterior portions of sterno-hyoid and sterno-thyroid). It differs from Gaskell’s classification in that the temporal, masseter, pterygoids (V), posterior digastric and stylo-hyoid (VII), sterno-mastoid and trapezius (XI spinal) are held to be somatic, and that the tongue muscles (XII) are considered to be splanchnic structures. Evidence for these views was sought by tracing the development of the muscles in question.

#### iv. DEVELOPMENT OF CERTAIN CRANIAL MUSCLES.

The rabbit was first taken, and an endeavour made to trace the first formation of the muscles of the head, but it was found that they develop so relatively late from what appears to be indifferent mesoblast that the question could not be decided. The tadpole of the toad was subsequently investigated, with the results which are here described.

Before giving a detailed account of the phenomena observed, it is to be remarked that Van Wijhe<sup>1</sup> states that in Elasmobranchs no muscles are developed from the myotomes of the 4th and 5th cranial segments (*i.e.*, that the V and VII nerves supply no somatic muscles), whilst the myotome of the 6th cranial segment remains very rudimentary. He also states that the myotomes of the 7th, 8th, and 9th cranial segments give rise to “vom Schädel zum Schultergürtel ziehende Muskeln nebst dem vordersten Theile des Sternohyoideus.”

<sup>1</sup> “Über die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes.”

The tadpoles were fixed in a solution of mercuric perchloride, stained in borax-carmin, imbedded in paraffin, and cut into serial sections in various planes.

In the earliest stage depicted,  $2\frac{1}{2}$  mm. in length, transverse and longitudinal sections (*vide* figs. 1 and 13) show that there are three gill-slits, the hyo-mandibular and 1st and 2nd branchial, and that the mesoderm of the head forms a continuous sheet on either side the gut, with no trace of a body-cavity.

By the time the embryo has attained a length of  $2\frac{1}{2}$  mm. a split has appeared in the ventral part of the mesoderm of the 6th and succeeding segments, the cavity of which is continuous with the pleuro-peritoneal cavity behind, of which it forms the anterior portion.

No trace of a body-cavity is found at any stage of development in the dorsal portions of any of the segments of the head, or in the ventral portions of the 4th and 5th head segments.

Successive gill-slits are formed behind the first three, and when the tadpole has reached the length of 3 mm. there are five—the hyo-mandibular and the 1st, 2nd, 3rd, and 4th branchial (fig. 2). This figure also shows that there is a progressive retardation from before backward in the aggregation of cells to form the myotomes of the respective segments). When the tadpole is  $2\frac{1}{2}$  mm. long the mesoderm of the 4th segment forms, on either side of the gut, a continuous sheet, the cells of which are all alike (figs. 3 and 4). At a length of 3 mm. the differentiation of the mesoderm of the 4th segment has begun, and there is on either side of the gut a long vertically placed strip of cells, more closely aggregated together than the rest of the mesoderm on each side of the strip (figs. 5 and 6). The outer side of this strip of aggregated cells is more sharply defined than its inner side, and nuclei in a state of karyokinesis are more frequent in it than in the rest of the mesoderm. As will be shown below, this band of cells is the first definite trace of certain of the muscles which are developed in this segment.

The band is better defined and more clearly marked off from the rest of the mesoderm when the tadpole has attained a length of 4 mm. (fig. 7). By the time the tadpole is  $4\frac{1}{2}$  mm. long it is seen that the band has separated into two portions,—an upper,

situated dorso-lateral and lateral to the gut, and a lower, situated ventro-lateral to the gut (fig. 8).

A similar series of changes takes place in the 5th cranial segment. At a length of  $2\frac{1}{2}$  mm. there is a layer of undifferentiated mesoderm on either side of the gut (*vide* fig. 9). When the tadpole is 3 mm. long, this has separated into a vertical band of closely-packed cells, on each side of which the mesoderm is looser in texture (fig. 10). The hyo-mandibular cleft is seen in this section, and it appears as if the vertically-placed strip were outside the gill-cleft: this appearance is due to the fact that the hyo-mandibular cleft projects forwards as well as outwards (*vide* fig. 2). In fig. 11, from a tadpole 4 mm. in length, the section depicted is relatively a little more caudalwards, and just behind the springing of the hyo-mandibular cleft.

By the time the tadpole is  $4\frac{1}{2}$  mm. long (fig. 12) this vertically placed band of mesoderm has nearly separated<sup>1</sup> into an upper and lower portion, the upper situated dorso-laterally, the lower ventro-laterally of the gut, exactly as in the case of the 4th segment.

The mesoderm of the 6th cranial segment, when the tadpole is  $2\frac{1}{4}$  mm. long, is undifferentiated, and there is no pleuro-peritoneal cavity (fig. 13). Shortly afterwards a slit appears in the ventro-lateral portion of the mesoderm—the beginning of the body-cavity in this segment (fig. 14, from a tadpole  $2\frac{1}{2}$  mm. long).

The mesoderm dorsal to the body-cavity, by the time the tadpole is 3 mm. long, has separated into a closely packed strip of cells, on each side of which are a few scattered ones (fig. 15). This strip is better marked when the tadpole is 4 mm. in length (fig. 16).

The mesoderm of the 7th segment is barely formed when the tadpole is  $2\frac{1}{4}$  mm. long (fig. 1). As it grows in length the mesoderm of the 7th segment is seen, in transverse sections of a tadpole  $2\frac{1}{2}$  mm. long, to be a uniform band of mesoderm just behind the 2nd branchial cleft, whilst there is a body-cavity in the ventro-lateral portion (fig. 17).

When the tadpole is 3 mm. in length, the mesoderm of the

<sup>1</sup> The figure shows that the separation is complete, but a little further back (*vide* fig. 48—taken from the same tadpole) it is incomplete.

7th segment, dorsal to that portion where the pleuro-peritoneal cavity has appeared, has differentiated into a central closely-packed mass, on either side of which are a few scattered cells (fig. 18). The process has advanced further by the time the tadpole is 4 mm. long (fig. 19).

Longitudinal horizontal sections show that a similar process takes place in the 8th and 9th segments, and that the ventral portions of the successive strips of packed mesoderm cells of the 7th, 8th, and 9th are early united together from before backwards to form a continuous sheet (figs. 24 and 25).

These strips of aggregated mesoderm cells are the rudiments of certain cranial muscles, the development of which will be subsequently traced, but before doing so their morphological value must be considered.

It is clear that the lower portions of the bands in the 4th and 5th segments, which have separated off from the upper portions by the time the tadpole has attained a length of  $4\frac{1}{2}$  mm., are situated ventro-laterally to the gut, and correspond in part to the 'Seitenplatten' of v. Wijhe, *i.e.*, are splanchnic.

The upper portions on either side of the gut, both of these and of the succeeding segments, might be regarded as either an upper splanchnic portion, or represent the myotomes of v. Wijhe, *i.e.*, might be somatic.

In favour of the former view there is the statement of v. Wijhe, as mentioned above, that in Elasmobranchs the myotomes of the 4th and 5th segments atrophy early in development, and the myotome of the 6th segment remains very rudimentary.

On the other hand, it is much more probable that they are somatic, corresponding to the myotomes of Elasmobranchs, and for the following reasons.

If these dorsal portions represent splanchnic structures only, it might be expected that some rudiments of aggregations of cells would appear dorsal to them, and then vanish: this does not happen.

Again, the upper limit of the dorso-lateral strip of cells in, say, the 4th segment (fig. 5) is exactly similar to that depicted by v. Wijhe in the case of the myotomes of Elasmobranchs; the difference lies only in the fact that the lower limit of this dorso-lateral strip extends more ventrally in

the tadpole than in the Elasmobranch. And, lastly, v. Wijhe says, as quoted above, that in Elasmobranchs the anterior portion of the sterno-hyoid is developed from the myotomes of the 7th, 8th, and 9th segments. Now, as will be shown below, the dorso-lateral strips of cells of the 7th, 8th, and 9th segments of the tadpole give origin to the genio-hyoid, sterno-hyoid and omo-hyoid. Hence it is fairly certain that they are somatic, and therefore the similarly situated muscle-rudiments in the 6th, 5th, and 4th segments are also somatic. Compare fig. 19 (7th segment) with figs. 16 (6th segment), 12 (5th segment), and 8 (4th segment). It is concluded that the myotomes of the 4th, 5th, and 6th segments do not atrophy or remain rudimentary in the tadpole as they do in the Elasmobranch, but persist and develop into muscles, as will now be shown.

The further development of the muscles may be conveniently taken in groups, and those of the 4th and 5th segments first of all. The changes undergone by the ventro-lateral groups of mesoblast cells are simple. Their lateral ends become attached to Meckel's cartilage and the cerato-hyal respectively, and their inner ends join together, forming the meckelian and hyoidean mylo-hyoid muscles (*vide* figs. 24, 25, 26-32, 39-41). The meckelian mylo-hyoid is a thin broad sheet, whilst the hyoidean mylo-hyoid is a thick band of muscle. One or two of the posterior fibres of the hyoidean mylo-hyoid become attached to the 1st branchial cartilage.

During metamorphosis these two muscles fuse together to form the mylo-hyoid muscle of the toad (*vide* figs. 63, 64), which differs from that of mammals in that it has a hyoidean as well as a meckelian portion, and is innervated by the VII as well as by the V nerve.

The myotome of the 4th segment, which is at first placed dorso-ventrally, soon becomes tilted so that its dorsal end is more posterior than its ventral extremity. This process, which is fairly evident in fig. 7, from a tadpole 4 mm. long, is very marked by the time a length of  $4\frac{1}{2}$  mm. is attained (figs. 21-25). It results in the myotome lying across and on the inner side of the myotome of the 5th segment.

The 4th myotome gradually becomes separated into two, the anterior digastric muscle, passing from the outside and inner

surface of the suspensorium to Meckel's cartilage, and a long strip of muscle lying on the inside of the suspensorium, with its front end attached to the dorsal surface of Meckel's cartilage (*vide* figs. 21–25). This long strip becomes divided into three portions,—the pterygoid, which arises posteriorly from the under surface of the pedicle of the suspensorium, and the temporal and masseter, which arise from the inner surface of the suspensorium, and from the dorsal surface of its pedicle (*vide* figs. 26–32 and 33–41).

The myotome of the 5th segment develops into (1) the posterior digastric muscle, which passes from the outside of the orbital process of the suspensorium to the top of the cerato-hyal, and (2) a muscle which, lying just below the anterior digastric, passes from the cerato-hyal to Meckel's cartilage (*vide* figs. 20–23, 28–32, and 33–36).

This condition of the muscles, developed thus early in tadpole life, persists until metamorphosis begins. The changes which then take place occur concurrently with those in the cartilages. Meckel's cartilage elongates backwards, so that from being a small mass attached to the front end of the suspensorium, it becomes a long bar directed antero-posteriorly; at the same time the front end of the suspensorium rotates downwards and backwards, and its orbital process atrophies.<sup>1</sup>

The beginning of the changes in the muscles is seen in figs. 42–46. Little alteration takes place in the relative position of the muscles on the inner surface of the suspensorium; the pterygoid is seen to be attached to the inside edge of Meckel's cartilage, whilst the masseter and temporal are inserted into its outside edge. The muscle which, developed from the 5th myotome, connects together the cerato-hyal and Meckel's cartilage, atrophies early in metamorphosis. The greatest change takes place in the posterior digastric: as the orbital process of the suspensorium atrophies, the upper end of the posterior digastric extends upwards to the roof of the skull, whilst its lower end loses its attachment to the top of the cerato-hyal and becomes fixed to the hind end of the now elongated Meckel's cartilage. The anterior digastric, owing to this forward movement of the posterior digastric and the elongation backwards of Meckel's

<sup>1</sup> *Vide* Balfour. *Comp. Embry.*, vol. ii.



cartilage, now lies on the inner side of the latter muscle, and the two muscles together form the depressor mandibulæ of the toad, which is innervated by the Vth and VIIth nerves.

The myotome of the 6th segment was left as a mass of cells lying lateral to the gut, just behind the 1st branchial cleft (*vide* figs. 16 and 47, from tadpoles 4 mm. long). It gradually becomes divided into an upper and lower portion (*vide* figs. 48–50, from a tadpole 4½ mm. long), the former of which becomes the most anterior petro-hyoid muscle (*vide* figs. 50 and 51), whilst the latter assumes a more and more ventral position (*vide* fig. 25). From this lower portion is formed a muscle which connects the ventral end of the 2nd branchial cartilage to the upper surface of the cerato-hyal cartilage (*vide* fig. 39). This muscle persists during the whole of tadpole life, and only disappears as metamorphosis comes on.

The myotomes of the 7th, 8th, and 9th segments were left as strips of cells lying laterally to the gut (*vide* fig. 19, from a tadpole 4 mm. long). From these myotomes two sets of muscles are developed: from the upper ends are formed the 2nd, 3rd, and 4th petro-hyoid muscles (*vide* figs. 51–53, 56, and 57), exactly as in the case of the 6th segment; whilst the lower portions shift ventrally so as to lie dorso-laterally to the pleuro-peritoneal cavity between this and the developing branchial chamber (*vide* figs. 24, 25, 55, and 56). The lower portion of the myotome of the 7th segment forms the genio-hyoid muscle; its front end rapidly extends forward (*vide* fig. 54) and becomes attached to the inferior labial cartilage, whilst its hind end is fixed to the basi-branchial plate (*vide* fig. 41). No further change in the position and connections of the genio-hyoid muscle takes place during tadpole life; shortly before metamorphosis, its anterior portion divides into two parallel slips, an inner and outer (*vide* figs. 42–46, 63, 64). As metamorphosis comes on, the inferior labial cartilage disappears, and the front end of the genio-hyoid becomes attached to the anterior extremity of Meckel's cartilage (*vide* figs. 63, 64).

The lower portions of the 8th and 9th myotomes fuse antero-posteriorly (*vide* figs. 24 and 25), and form a strip of cells occupying at first the same position in regard to the pleuro-peritoneal cavity and branchial chamber as the genio-hyoid. Subsequently,



its hind end assumes a still more ventral position, and figs. 40 and 57 show the strip of cells as a flattish band of muscle between the pleuro-peritoneal cavity and the branchial chamber, with its posterior end more ventral than its front end, which is attached to the ventral end of the 3rd branchial cartilage. Very little further change takes place until the development of the shoulder girdle, shortly before metamorphosis, when the posterior end of the band of muscle, hitherto free, becomes attached to it, the lateral edge forming the omo-hyoid, and the median the sterno-hyoid (*vide* fig. 71). A few fibres of these muscles are continued forward into the genio-hyoid, but the main mass is inserted into the hyoid plate.

It would appear, then, that the ventral longitudinal muscles of the neck are formed from the ventral portions of the myotomes of the 7th, 8th, and 9th segments; they originate, at about the same period, by a downward shifting from their respective myotomes,—the genio-hyoid from the 7th, the sterno- and omo-hyoid from the 8th and 9th segments. Whereas the genio-hyoid early assumes its permanent form, the sterno- and omo-hyoid only do so later, on the development of the shoulder girdle. These facts may be correlated with the early importance of the jaws and the late development of the shoulder girdle in the tadpole.

On comparing the development of the sterno- and omo-hyoid in the Elasmobranch and the tadpole, a difference is found to exist. In the former, v. Wijhe says, as quoted above, that the 7th, 8th, and 9th myotomes give rise to the fore part of the sterno-hyoid and to muscles passing from the skull to the shoulder girdle. In the tadpole no muscles other than the 2nd, 3rd, and 4th petro-hyoids and the genio-sterno- and omo-hyoid are formed from the 7th, 8th, and 9th myotomes of the head, and no elements are added to the hind ends of the latter muscles from the myotomes of the trunk. The sterno- and omo-hyoid are the representatives in the head of the ventral longitudinal muscles of the trunk, and the explanation of the difference between the tadpole and the Elasmobranch in their development possibly lies in the very anterior position of the shoulder girdle in the former animal. Thus the scapula, when

first formed, lies directly over the transverse process of the 1st cervical vertebra in the tadpole.

*Tongue muscles.*—No trace of the tongue muscles is seen until shortly before metamorphosis begins. Thus in longitudinal and transverse sections of tadpoles 14 mm. in length (figs. 58 and 59) the genio-hyoid muscle is seen passing from the 1st basi-branchial cartilage to the inferior labial cartilage, whilst there are a few scattered cells only below the buccal epithelium, lying between the basi-hyal and Meckel's cartilages, and well above the genio-hyoid muscle. Soon after the hind legs have appeared, these cells are seen to have proliferated, forming a mass below the epithelium of the floor of the mouth, and from this mass there is an outgrowth backwards to form the hyo-glossus muscle (figs. 60 and 61). A little later (fig. 62) the hyo-glossus is seen to have extended backwards, and an outgrowth spreading forwards, to form the genio-glossus, has appeared, and the protuberance of the tongue is greater. In the tadpole with well developed hind legs it is seen (figs. 63 and 64) that the hyo-glossus has spread backwards, and is attached to the hind edge of the hyoid plate internal to the genio-hyoid, and that the front end of the genio-glossus has extended forwards to Meckel's cartilage, whilst the tongue is much greater in bulk.

The tongue, then, together with the genio-glossus and hyo-glossus, begins to be developed late in the tadpole stage, and only becomes completely formed just before the front legs appear externally. It is not developed, as is generally held, from the front end of the ventral longitudinal muscles,<sup>1</sup> but is quite independent in origin, being derived from cells lying between Meckel's cartilages and the basi-hyal, just beneath the epithelium of the floor of the mouth, from cells, which can be traced from the tadpole stage of 2½ mm. in length, lying dorsal to the mylo-hyoid between this and the floor of the mouth (*cp.* figs. 28, 8, 6, 5).

It is concluded that the tongue, genio-glossus, and hyo-glossus are splanchnic in origin, inasmuch as they are developed from that portion of mesoblast, ventral and ventro-lateral to the gut, which does not develop into the mylo-hyoid. It is by reason of this, and also because of the development of the submentalis

<sup>1</sup> *Vide* Wiedersheim. *Comp. Anat. of Vertebrates*, trans. by Parker.

at about the same period from the splanchnic mesoblast just in front of the tongue (*vide* figs. 62-64), that the masses of mesoblast cells which develop into the mylo-hyoid muscle cannot be considered to represent altogether the 'Seitenplatten' of Elasmobranchs in these segments.

The sections do not show whether the tongue is derived solely from the 4th, or from both this and the 5th segment; its development takes place too late in the life-history of the tadpole. The growth of the genio-glossus and hyo-glossus respectively, forward and backward, suggest that possibly mesoblast cells from both segments play a part in their origin.

*Laryngeal muscles.*—The larynx is formed as a median pouch in the ventral wall of the gut, in the region of the 4th branchial arch. It first becomes visible when the tadpole is 5 mm. long. Similarly, at the same stage, a trace of the laryngeal muscles is first seen; they are developed from hitherto undifferentiated mesoblast cells lying ventral to the gut, between this and the pericardium, on either side of the median laryngeal diverticulum (*vide* fig. 72). The position of these cells in relation to the gut is the same as that of the cells from which the tongue muscles are developed. Both the larynx and the laryngeal muscles remain rudimentary until shortly before metamorphosis (*vide* fig. 71). The laryngeal muscles, then, are developed from the splanchnic mesoblast of the 9th segment of the head.

*Sterno-mastoid and Trapezius.*—No trace of the sterno-mastoid and trapezius muscles is visible until a very late stage in tadpole life. Thus, in figs. 65-67, from a tadpole 14 mm. long, it is seen that the trunk myotomes do not reach quite up to the back of the auditory capsule, and that just outside the pronephros there is the beginning of a fore limb. There is no scapula, and no trapezius nor sterno-mastoid muscle. By the time the hind legs have appeared, the first trunk myotome has become attached to the back of the skull (fig. 68), but is still undifferentiated. At a little later stage, in which there are small hind legs (figs. 69, 70), the first trunk myotome has split up into portions, of which the following (in fig. 69) may be distinguished. Just outside the medulla there is, dorsally, a portion of the myotome simple and undivided, and at its foot there are three muscles which pass from the skull to the transverse portion of the 1st cervical

vertebra; whilst more to the side three masses of muscles can be distinguished, of which the dorsal one is the trapezius, the middle one the sterno-mastoid, and the lower one the levator anguli scapulæ. In fig. 70, a little further back, the scapula is visible, the trapezius, sterno-mastoid, and levator anguli scapulæ have already been inserted into the scapula, whilst the two outer of the muscles passing from the skull to the transverse process of the 1st cervical vertebra have united, so that there are two muscle masses only at the foot of the undivided portion of the myotome. In fig. 71, taken from a tadpole with large hind legs, the insertion of the sterno-mastoid into the anterior border of the scapula can be seen on the right hand side, whilst on the left (which is a little more anterior) the trapezius and sterno-mastoid are seen nearer their point of origin.

The sterno-mastoid and trapezius are thus absent during the greater part of tadpole life. They are developed from the 1st trunk myotome as metamorphosis comes on, in correlation with the appearance of the scapula. They are therefore not splanchnic, but somatic in origin.

On surveying the development of the myotomes of the head, it is clear, in the first place, that from each of the 8th and 9th myotomes (3rd and 4th branchial) is developed dorsally a petro-hyoid muscle, and ventrally a constituent of the strip of muscle, which becomes the sterno-hyoid and omo-hyoid. Similarly, from the myotome of the 7th segment (2nd branchial) is developed dorsally a petro-hyoid muscle, and ventrally the genio-hyoid muscle. Similarly, again, from the myotome of the 6th segment (1st branchial) is developed dorsally the foremost petro-hyoid muscle, and ventrally the muscle which passes from the 2nd branchial cartilage to the cerato-hyal, which muscle, however, has only a larval existence. In the next succeeding segments, the 5th and 4th (hyoid and maxillary), such a division of the myotomes into a dorsal and ventral portion is not so obvious, possibly by reason of the changes dependent on the development of a suctorial mouth. The 4th and 5th myotomes, like those which follow, are at first placed vertically, but the 4th soon rotates about a horizontal transverse axis, so as to lie on the inner side of and across the 5th myotome. The

5th myotome separates into the posterior digastric (which has much the same position as the petro-hyoid muscles, only differing in that its upper end is attached to the orbital process of the suspensorium), and into the muscle connecting the cerato-hyal to Meckel's cartilage, but whether the latter is to be regarded as a forward continuation of the ventrally placed portions of the branchial myotomes seems doubtful. Like the muscle developed from the ventral portion of the 6th myotome, the muscle connecting the cerato-hyal to Meckel's cartilage has only a larval existence. There is no trace of a dorso-ventral division of the 4th myotome, unless the anterior digastric, which is separated off from its front (morphologically ventral) end, be regarded as the ventral part equivalent to those in the branchial segments. Determination, by experiment, of the existence or absence of posterior root-ganglion fibres for this muscle would shed light on the question. If they are present, the anterior digastric may be regarded as the ventral part of the 4th myotome, and the most anterior representative of the ventral longitudinal muscles. The rest of the 4th myotomes becomes split up longitudinally into the temporal, masseter, and pterygoid muscles.

In regard to the muscles which originate in the splanchnic portions of the head segments, the mylo-hyoid is early developed in the 4th and 5th segments, while later on, towards the end of larval life, the submentalis is developed in the 4th, and the tongue muscles (intrinsic and extrinsic) from the 4th and (?) 5th segments. No skeletal muscles are developed in the splanchnic portions of the 6th, 7th, and 8th (1st, 2nd, and 3rd branchial) segments, whilst in that of the 9th (4th branchial) the laryngeal muscles can be seen at an early stage, though undergoing but little development until shortly before metamorphosis.

There are certain differences between the head muscles of the toad and the dog: there are, for instance, muscles which exist in the tadpole only, but not in the toad or dog, viz., the muscle connecting the cerato-hyal to Meckel's cartilage, and that connecting the 2nd branchial cartilage to the cerato-hyal. The petro-hyoid muscles of the toad are absent in the dog. In the toad there is one pterygoid muscle, in the dog two, and the anterior digastric is differently placed. In the dog there is the

stylo-hyoid muscle, not present in the toad, lying alongside the posterior digastric, and, like it, innervated by the facial nerve. The ordinarily accepted view that this muscle is delaminated from the posterior digastric is supported by the facts that the size of its nerve fibres is the same as that of those going to the latter muscle, and that it has no posterior root ganglion fibres. Again, the hyoid constituent of the mylo-hyoid muscle is wanting in the dog.

The tongue is more complex in the dog than the toad: the tongue of the latter is the representative only of the tuberculum impar<sup>1</sup> of the dog, and similarly grows upwards in the floor of the mouth, between the ventral ends of the maxillary and hyoid arches, whilst the part derived in the dog from the hyoid and 1st branchial arches (furcula) is not developed. Such a view is supported by consideration of the origin of the sensory nerves of the tongue in the two animals; and by the fact that in the toad the duct of the thyroid gland, though disappearing before the development of the tongue begins, yet opens into the mouth just in front of the basi-hyal, and so behind the tongue. The extrinsic muscles of the tongue are also more complicated in the dog than the toad: in the latter they consist of the hyo-glossus and genio-glossus only, whilst in the dog there is additionally the stylo-glossus. It may be inferred that the intrinsic muscles of the tongue in the dog are developed from the 4th, 5th, and 6th, and the extrinsic muscles from the 4th and 5th segments.

The stylo-pharyngeus, crico-thyroid, palato-pharyngeus, constrictors of the pharynx, levator veli palatini, azygos uvulae, present in the dog, are absent in the toad, and their morphological position can only be inferred from their nerve supply; and similarly in the case of the tensor tympani and tensor veli palatini.

The trapezius and sterno-mastoid muscles in the toad are developed from the first trunk myotome only, whereas in the dog the extended origin of the spinal portion of the XIth nerve suggests that possibly in that animal they are developed from some of the succeeding trunk myotomes as well.

The ventral longitudinal muscles of the neck are a little different in the two animals. In the toad they consist of the

<sup>1</sup> *Vide* Quain, vol. i. pt. i.

genio-hyoid, sterno-hyoid, and omo-hyoid, whilst in the dog the omo-hyoid is absent, and there is a deeper muscle layer, consisting of the thyro-hyoid and sterno-thyroid. A more important question is the origin of these muscles in the dog. In the toad they are developed from head myotomes only, whereas in the dog it is possible that, like the Elasmobranch, the posterior portions of these muscles are derived from trunk myotomes. As suggested above, the difference is possibly connected with the relative position of the shoulder girdle.

Of the somatic muscles of the head of the dog, only the ventral longitudinal ones have posterior root ganglion fibres.<sup>1</sup> The causes of these differences are obscure, and but little light is shed on the problem by the fact of the development of the latter muscles from the ventral ends of the myotomes from which they are derived, and by the consideration that they are the representatives in the head of the ventral longitudinal muscles of the trunk. And the difficulty is accentuated by the fact that no posterior root ganglion fibres accompany the spinal part of the XIth nerve.<sup>2</sup>

Notwithstanding, then, the differences between the head muscles of the toad and the dog, it would seem a legitimate deduction from the above that in the latter animal the temporal, pterygoids, masseter, anterior digastric, posterior digastric, and stylo-hyoid, sterno-mastoid, and trapezius muscles are somatic, whilst the tongue muscles (intrinsic and extrinsic) are splanchnic in origin, as indeed the maximum size of their motor fibres suggested.

The following classification of the muscles of the head of the dog can be made from the above:—

## V. CLASSIFICATION OF CRANIAL MOTOR NUCLEI.

One or two conclusions result from the foregoing as to the cranial nuclei which innervate cross-striped muscles.

<sup>1</sup> With the doubtful exception of the anterior digastric; see above.

<sup>2</sup> The sterno-mastoid and trapezius muscles, however, possibly have posterior root ganglion fibres entering them with the additional motor supply from the 1st, 2nd, and 3rd cervical nerves, discovered by Risien Russell, *Brain*, 1897.

| Segment                    | Somatic.<br><br>Their motor fibres have a maximum diameter of 16 $\mu$ .                    | Splanchnic.<br><br>Their motor fibres have a maximum diameter of 11·2 $\mu$ .   |
|----------------------------|---|---|
| 1.                         | Rect. sup., Lev. palp. sup., Rect. inf. and int.,<br>Obliq. inf.<br>iii                     | 0   |
| 2.                         | Obliq. sup.<br>iv   | 0   |
| 3.                         | Rect. ext. and Retract. oculi<br>vi   | 0   |
| 4. (maxillary)             | Temporal, masseter, pterygoids, anterior<br>digastric<br>v                                  | Mylo-hyoid, tensor tym-<br>pani, tensor veli palatini v                         |
| 5. (hyoid)                 | Posterior digastric, stylo-hyoid<br>vii   | Other facial muscles vii  |
| 6. (1st branchial)         | . . . . . 0 . . . . .<br>.  | Stylo-pharyngeus ix<br>Crico-thyroid  |
| 7. (2nd branchial)         | Genio-hyoid<br>xii  | Palato-phary., Constrict. pharyngei<br>Levator veli palatini<br>Azygos uvulae x |
| 8. (3rd branchial)         | ) Sterno-hyoid<br>Sterno-thyroid (1 anterior part only) xii and 1st cervical<br>Thyro-hyoid | Laryngeal muscles (9th segment) xi medullary                                    |
| 9. (4th branchial)         |   |   |
| 1st cervical<br>(1st only) | Sterno-mastoid and trapezius<br>xi spinal   |   |



It was held by Gaskell<sup>1</sup> that the motor nuclei in the mid and hind brain can be arranged as follows:— $\alpha$ , an anterior cell column, a continuation of the spinal anterior cornu, formed by the XII, VI, IV, and III nuclei; and  $\beta$ , a lateral cell column, a continuation of the lateral horn of the spinal cord, formed by the XI spinal, nucleus ambiguus of the XI, medullary X and IX, the VII and the V.

If, however, they be arranged according to the above proposed revision of the morphological position of some of these muscles, we should have the following classification of the nuclei according, in Hughlings Jackson's phrase, to the muscles they 'represent':— $\alpha$ , a cell column innervating muscles developed in the somatic portions of the head segments; and  $\beta$ , a cell column innervating those muscles developed in the splanchnic portions of the head segments, *i.e.*, corresponding to the table given above.

The cell-column  $\alpha$  will be homologous with the anterior cornual cells. Correspondingly, it is found that the maximum size of the large fibres in the spinal anterior roots in the non-limb regions of the spinal cord is the same as that of the nerve fibres passing to the somatic muscles in the cranial region. (In the region of the limbs, however, the maximum diameter of the fibres in the anterior spinal roots is greater—in the specimens examined as much as 20.8  $\mu$ .) Cell-column  $\beta$  will be homologous with the lateral cornual cells of the spinal cord innervating splanchnic muscles.

Whereas splanchnic muscles in the body are not cross-striated, those in the head are cross-striated. And insomuch as this development of cross-striated muscles in the splanchnic mesoderm of the head may in all probability be connected with the development of the branchial bars there, the term 'branchial' may perhaps be applied to their motor nerve-fibres and nuclei of origin, in place of 'non-ganglionated splanchnic' employed by Gaskell.

The motor fibres of the cranial nerves, with exception of the hypoglossal, innervate cross-striated muscles developed in the corresponding segments only. The hypoglossal, on the other hand, is the nerve of no individual segment, but innervates

<sup>1</sup> *Loc. cit.*

splanchnic muscles developed in the 4th, 5th, and 6th, and somatic muscles, derived from the 7th, 8th, and 9th, segments.

The motor fibres of the IX, X, and medullary XI innervate two sets of splanchnic muscles, cross-striped and unstriped; and it is stated by Gaskell<sup>1</sup> that the n. ambiguus is the motor nucleus of the former, the dorsal nucleus that of the latter.<sup>2</sup> There is, then, in regard to these nerves an overlapping of splanchnic nuclei of cross-striped and involuntary muscles, but it is to be remarked that the latter muscles, other than the cardiac, are developed from body, not head, segments.

The sterno-mastoid and trapezius are cervical, not head muscles; they are developed from the 1st trunk myotome in the toad, possibly from more than one in the dog; and correspondingly their nerve, the external portion of the XI, arises from the spinal cord.

The above results suggest that it should be possible to split up the Vth, VIth, and XIIth nuclei, each into two portions, supplying somatic and branchial muscles respectively. Though this can only be determined by the application of v. Gudden's or Nissl's methods, yet there are already indications that it may be possible.

Kölliker<sup>3</sup> holds that the descending root of the V is motor, and goes on to remark, "welche Muskeln dieser Wurzel untersteht ist freilich nicht von Ferne zu errathen, doch darf man vielleicht an den Tensor veli palatini und den Tensor tympani denken, schwerlich an den Mylo-hyoideus und Biventer anterior." And Tooth and Turner<sup>4</sup> state that in a case of atrophy of the masticatory muscles, the motor nucleus of the V was found to be atrophied.

This suggests that the descending root of the V supplies the branchial muscles, mylo-hyoid, tensor veli palatini, and tensor tympani; whilst the somatic muscles—temporal, masseter, pterygoids, and anterior digastric—are innervated by the main nucleus of the V.

<sup>1</sup> *Loc. cit.*

<sup>2</sup> This theory, that the dorsal nucleus is motor to unstriped muscles, has been confirmed by Marinesco (*Comptes rendus de la Société de Biologie*, 1897), by Bruce (*Brain*, 1898), and by Van Gehuchten (*Jour. de Neurologie*, 1898).

<sup>3</sup> *Handbuch der Gewebelehre des Menschen.*

<sup>4</sup> *Brain*, 1891. They do not, however, say whether the anterior digastric muscle was atrophied or not.

From the recent researches of Van Gehuchten<sup>1</sup> on the nucleus of the VII, it may be inferred that the somatic muscles (posterior digastric and stylo-hyoid) are innervated by a portion of the external-inferior division, and the other, branchial, muscles by the remainder of the facial nucleus.

As to the XII nucleus, it is possible that whereas the tongue muscles are innervated by the hypoglossal nucleus proper, the somatic muscles (genio-hyoid in the monkey; this together with the thyro-hyoid and anterior portions of the sterno-hyoid and sterno-thyroid in the dog) are innervated from the front end of the anterior cornu of the spinal cord, which sends fibres into the hypoglossal.<sup>2</sup>

#### vi. COLLATERAL EVIDENCE FROM DISEASE.

There are a few obscure cases of disease of the motor nuclei in the mid and hind brain, which are of interest in connection with this classification of them.

Thus, somatic nuclei occasionally atrophy in common; *e.g.*, in the patient of Ferrier, whose case was published by Hughlings Jackson,<sup>3</sup> external ophthalmo-plegia and atrophy of the masticatory muscles occurred.

On the other hand, Hughlings Jackson<sup>4</sup> states that paralysis of the orbicularis palpebrarum is rare in cases of ophthalmo-plegia externa; now, whereas the external ocular muscles are somatic, the orbicularis palpebrarum is branchial in origin. In bulbar paralysis the atrophy affects primarily branchial nuclei, and only rarely spreads to the somatic nuclei of the V, VI, IV, and III nerves.

In some cases of congenital ptosis contraction of the levator palpebræ superioris—a somatic muscle—takes place on certain movements. It is of interest to note that these movements are all executed<sup>5</sup> at least in part by somatic muscles, for they are

<sup>1</sup> *Jour. de Neurologie*, Mars 20, 1898.

<sup>2</sup> *Op. fast* that the largest fibres in the hypo-glossal roots are found in the hind-most ones only.

<sup>3</sup> *Lancet*, 1893.

<sup>4</sup> *Loc. cit.*

<sup>5</sup> Hughlings Jackson, *Lancet*, 1894; Gunn, *Trans. Oph. Soc.*, vol. iii.; Sinclair, *Oph. Rev.*, 1898; Snell, *Sheff. Med. Jour.*, 1898; Swauzy, *Diseases of Eye*.

those of mastication, opening the mouth, and deglutition; whereas no cases are on record in which elevation of the upper lid has taken place in association with movements of branchial muscles only, *e.g.*, of the face, tongue, or larynx.

#### vii. SENSORY FIBRES OF THE CRANIAL NERVES.

The sensory branches of the cranial nerves may be separated into two divisions by the maximum size of the nerve fibres they contain. Medullated nerve fibres of all diameters up to  $16\ \mu$  are found in the frontal, long ciliary, ethmoidal, and infra-trochlear from the 1st division of the V; the lacrymal, infra-orbital, subcutaneous malæ, dental branches of the infra-orbital, palatinus major, and nasalis posterior, from the 2nd division of the V; the auriculo-temporal, buccal, terminal (skin) branches of mylo-hyoid, mental and dental branches of inferior dental, from the 3rd division of the V; and the n. auricularis of the X.

Medullated fibres of all diameters up to  $11.2\ \mu$  are found in the palatinus minor, lingual, orbital gland branches of the buccal, parotid gland branches of the auriculo-temporal, chorda tympani, lingual branch of IX, superior laryngeal, communicans laryngei, cardiac and pulmonary branches of X, and vagus trunk beyond the pulmonary branches.

The maximum diameter of the fibres placed in the second division was in some cases as low as  $9.6\ \mu$ , in others as high as  $12.8\ \mu$ . The maximum diameter of the fibres placed in the first division varied between  $17.6\ \mu$  and  $14.4\ \mu$ . In three cases, the long ciliary, the mental branch of the inferior dental, and the skin branches of the mylo-hyoid (all of which are placed in the 1st division), it was very occasionally found that the maximum diameter of the fibres might be as low as  $12.8\ \mu$ ; but insomuch as the variations in the maximum diameter of these nerve fibres are from this figure upwards only, it would appear that the two divisions of nerve fibres proposed are fairly distinct.

From a comparison of this with embryological evidence, it follows that ectodermal structures (skin, nasal epithelium, and stomodeum) have passing towards them fibres of various diameters up to  $16\ \mu$  as a maximum, whilst in the case of

endodermal structures the maximum diameter of the nerve fibres does not exceed  $11.2\ \mu$ . But to this there is an apparent exception—the salivary glands have only the smaller sized fibres passing to them, though developed, according to received opinion, from the stomodeum.<sup>1</sup> This ordinarily accepted view, as far as I can learn, is based on evidence from comparative anatomy, and not from embryological investigation.

It seemed possible that the line of junction of epiblast and hypoblast on the floor and sides of the mouth might be found to be a little further forward than is thought, so that these glands might be hypoblastic in origin—as is suggested by the size of the nerve fibres. The point was investigated in the rabbit, but with inconclusive results. The line of junction of stomodeal epiblast and hypoblast ceased to be visible by the 12th day, whilst the salivary glands did not begin to develop until the 15th day of embryonic life.

The evidence cited above with regard to sensory fibres in the nerves of the cross-striped splanchnic muscles of the head goes to show that their maximum diameter is the same as that of the sensory fibres of the endoderm in the head region.

Sensory fibres of various diameters, up to a similar maximum, are found in the sympathetic, and pass to splanchnic structures.

It seems, then, possible to group all these fibres together as visceral sensory fibres, supplying both endoderm and splanchnic mesoderm.

The sensory fibres of the ectodermal structures of the head have a distinctly higher maximum of size than the visceral sensory fibres. (To this general statement, the nerves of the salivary glands form a doubtful exception.)

As regards the origin of the afferent fibres of the cranial nerves, it is to be noted that Gaskell<sup>2</sup> divided them into 'somatic afferent,' *i.e.* the ascending root of the trigeminal, and 'splanchnic afferent,' *i.e.* the ascending root of the vagus.

From the above described observations it would appear that there are three additional groups of sensory fibres to be accounted for—the splanchnic afferent fibres of the Vth (muscle sensory and sensory fibres of the splanchnic sensory branches, such as the lingual), the splanchnic afferent (muscle sensory

<sup>1</sup> Vide *Quain's Anatomy*, vol. i. pt. i.

<sup>2</sup> *Loc. cit.*

and sensory fibres of the chorda tympani) fibres of the VIIth, and the somatic afferent (n. auricularis) of the Xth nerves.

Bruce<sup>1</sup> has described the sensory root of the Vth as consisting of two portions on either side of the gelatinous substance of Rolando; and it is possible that the inner and smaller portion consists of the splanchnic afferent, and the outer and larger division of the somatic afferent fibres. The splanchnic afferent fibres of the VII, with the geniculate as their posterior root ganglion,<sup>2</sup> end as the ascending root of the facial;<sup>3</sup> whilst the central connections of the n. auricularis are very possibly to be found in those few fibres of the 'vagus' which, according to Ramon y Cajal,<sup>4</sup> on entering the medulla, turn aside to join the descending root, and apparently, from the picture, the outer descending root, of the V. If this be so, the central terminations of the somatic (ectodermal) and splanchnic afferent fibres of the cranial nerves are quite separate and distinct—all the ectodermal sensory fibres finding their way into the outer descending root of the V; whilst the splanchnic sensory fibres end in the inner descending root of the V, and the descending roots of the VII, IX, and X.

#### viii. GENERAL CONCLUSIONS.

The observations above described may be summed up as follows:—

1. Somatic muscles are developed from each segment of the head. Their motor nerve-fibres have a maximum diameter which is the same as that of those innervating somatic muscles of non-limb regions of the body.

2. Whereas the splanchnic mesoderm of the body develops unstriated muscles only, that of the head develops cross-striated

<sup>1</sup> "Nerve tracts of the mid and hind brain."

<sup>2</sup> Which, according to His (as stated by Schäfer, *Quain*, vol. i. pt. i.), is derived from the same ganglionic mass as that which furnishes the ganglia of the auditory nerve, and from which fibres grow centrally into the brain and peripherally along the nerve.

<sup>3</sup> *Vide* Kölliker, *loc. cit.*

<sup>4</sup> "Beiträge zum Studium des Medulla oblongata." It was not determined whether these fibres come from the glosso-pharyngeal or the vagus proper.

muscles.<sup>1</sup> This is probably primarily dependent on the presence of gill-arches in the head. The motor nerve-fibres of these branchial cross-striped muscles have a maximum diameter which is greater than that of those supplying the splanchnic unstriped muscles of the body, and less than that of those which pass to somatic muscles.

3. The somatic muscles of the head differ from those of the body in not possessing root ganglion muscle-sensory nerve-fibres. To this statement the anterior digastric is a doubtful, and the ventral longitudinal muscles a positive exception.

4. The splanchnic muscles of the head probably have muscle sensory fibres, the maximum diameter of which betrays their splanchnic destination; these form a particular group of the splanchnic sensory fibres.

5. The sensory fibres of the ectodermic structures of the head have a maximum diameter which is greater than that of the splanchnic sensory fibres. To this the nerves to the salivary glands form a doubtful exception.

6. The maximum diameter of the nerve-fibres, both motor and sensory, passing to any structure, is dependent on the morphological position of that structure, and not on the nature of the impulses carried by them.

I have, finally, to express my hearty thanks, to Dr Gaskell for much help and criticism, and to Prof. Weldon for advice in connection with the embryological work. It is, of course, scarcely necessary to say that my former teachers are not responsible for any errors, in fact or theory, on my part. I have also to thank Prof. Schäfer for permission to do an experiment in his laboratory, and Dr Aldren Turner for performing a most difficult operation for me.

The expenses of the investigation have been defrayed by a Government grant from the Royal Society.

<sup>1</sup> And also, in the branchial region, the heart muscle.

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## DESCRIPTION OF PLATES X.-XXII.

The outlines of the structures were drawn with a camera lucida ; figs. 4 and 6 under a magnification of Zeiss oc. 3, obj. D ; the others under one of oc. 3, obj. A.

## FIG.

1. Longitudinal horizontal section,  $2\frac{1}{4}$  mm. long.
2. Ditto, 3 mm. long.
3. Transverse section,  $2\frac{1}{2}$  mm. long, at level of 4th segment. Right side more anterior.
4. The right side of section 3, under higher power. The outline of each individual cell drawn under the camera lucida.
5. Transverse section, 3 mm. long, at level of 4th segment.
6. Right side of section 5, under higher power. The outline of each individual cell drawn.
7. Transverse section, 4 mm. long, at level of 4th segment. The right side of the section is a little anterior to the left.
8. Transverse section,  $4\frac{1}{2}$  mm. long, at level of 4th segment. The right side of the section is a little posterior to the left.
9. Transverse section,  $2\frac{1}{2}$  mm. long, at level of 5th segment.
10. Ditto, 3 mm. long, ditto.
11. Ditto, 4 mm. long, ditto. The right side of the section is a little anterior to the left.
12. Ditto, 5 mm. long, ditto. The left side is a little anterior to the right.
13. Transverse section,  $2\frac{1}{4}$  mm. long, at level of 6th segment.
14. Ditto,  $2\frac{1}{2}$  mm. long, ditto.
15. Ditto, 3 mm. long, ditto.
16. Ditto, 4 mm. long, ditto. The right side is a little anterior to the left.
17. Transverse section,  $2\frac{1}{2}$  mm. long, at level of 7th segment.
18. Ditto, 3 mm. long, ditto.
19. Ditto, 4 mm. long, ditto.
- 20-25. Serial vertical longitudinal sections through a tadpole  $4\frac{1}{2}$  mm. long, 20 being the most external.
- 26-32. Transverse vertical sections through tadpole 9 mm. long. The right side is the more anterior ; 19 is the front end.
- 33-41. Longitudinal serial sections through tadpole 9 mm. long ; 33 is the most external.
- 42-46. Transverse serial sections through tadpole in which hind legs are large ; 42 is the most anterior.



Fig.

47. Transverse section from tadpole 4 mm. long, in 5th and 6th segment. The left and ventral sides are more anterior; this section is of a tadpole of same length as fig. 16, but is drawn so as to render the appearances seen in figs. 48-50 more intelligible.
- 48-50. Transverse serial sections through tadpole  $4\frac{1}{2}$  mm. long, in 5th and 6th segments. The left and ventral sides are more anterior than the right and upper parts.
- 51-53. Longitudinal vertical serial sections through tadpole  $7\frac{1}{2}$  mm. long; 51 is the most external.
54. Longitudinal vertical section through tadpole 5 mm. long. The anterior end of the genio-hyoid here shown is its furthest forward limit; it does not extend further forwards in adjacent sections.
55. Transverse section through tadpole  $4\frac{1}{2}$  mm. long, at level of 7th segment. The left side is anterior to the right.
56. Transverse section, 6 mm. long, through 7th segment; the upper part of the figure is more anterior than the lower.
57. Ditto, 9 mm. long, through 8th segment.
58. Longitudinal section, 14 mm. long.
59. Transverse section, 14 mm. long. The left side is anterior to the right.
60. Longitudinal section through tadpole in which hind legs have just appeared.
61. Transverse section, ditto. The left side is anterior to the right.
62. Longitudinal section through tadpole in which hind legs are of moderate size.
- 63, 64. Longitudinal serial sections of tadpole in which hind legs are large; 63 is the more internal.
- 65-67. Transverse serial sections from tadpole 14 mm. long, through 1st trunk myotome.
68. Transverse section of tadpole in which hind legs are small, through 1st trunk myotome.
- 69, 70. Transverse serial sections of tadpole in which hind legs are of medium size, through 1st trunk myotome; 69 is the more anterior.
71. Transverse section through tadpole in which hind legs are large, through 1st trunk myotome. The left side of the section is anterior to the right.
72. Transverse section through tadpole  $5\frac{1}{2}$  mm. long. The upper and left-hand sides of the section are more posterior than the lower and right-hand sides.

- A.* auditory vesicle.  
*ad.* anterior digastric.  
  
*B.* brain.  
*b.c.* branchial chamber.  
*b.b.* basi-branchial.  
*br.* branchial arch.  
*br.1.* 1st branchial arch, etc.  
*b.b.p.* basi-hyo-branchial plate.  
*b.h.* basi-hyal.  
*b.s.* branchial cleft.  
*1 b.s.* 1st branchial cleft, etc.  
  
*c.h.* cerato-hyal.  
  
*E.* eye.  
*ec.* ectoderm.  
  
*f.l.* fore limb.  
  
*g.g.* genio-glossus.  
*g.h.* genio-hyoid.  
*g.h.i.* internal slip of genio-hyoid.  
*g.h.e.* external slip of genio-hyoid.  
  
*h.* heart.  
*h.g.* hyo-glossus.  
*h.s.* hyo-mandibular cleft.  
*hy.* hypoblast.  
  
*I.* infundibulum.  
*i.l.* inferior labial cartilage.  
  
*lev. ang. scap.* levator anguli scapula.  
  
*lar.* larynx.  
*lary,m.* laryngeal muscles.  
*l.* liver.  
  
*ma.* masseter.  
*m. 4.* myotome of 4th cranial segment, etc.
- me.* Meckel's cartilage.  
*mes.* mesoderm.  
*m.h.h.* hyoidean mylo-hyoid.  
*m.h.m.* meckelian mylo-hyoid.  
*m.m.h.* muscle connecting Meckel's cartilage to cerato-hyal.  
*m.b.h.* muscle connecting 2nd branchial to cerato-hyal.  
  
*N.* nose.  
*n.* notochord.  
  
*æ.* œsophagus.  
*o.s.* orbital process of suspensorium.  
*om.hy.* omo-hyoid.  
*p.* pedicle of suspensorium.  
*p.d.* posterior digastric.  
*per.* pericardium.  
*ph.* pharynx.  
*p.p.g.* palato-pterygoid bar.  
*pt.* pterygoid.  
*pr.* pronephros.  
*ppc.* pleuro-peritoneal cavity.  
*precor.* pre-coracoid.  
*pet.hy.* petro-hyoid.  
  
*S.* suspensorium.  
*sb.m.* sub-mentalis.  
*s.l.* superior labial cartilage.  
*scap.* scapula.  
*sterno.m.* sterno-mastoid.  
*st.hy.* sterno-hyoid.  
  
*tg.* tongue.  
*th.* thyroid.  
*tr.* trabecula.  
*tem.* temporal.  
*1 t.m.* 1st trunk myotome.  
*trap.* trapezius.

NOTE ON THE STAINING OF SECTIONS WHILE EMBEDDED IN PARAFFIN. By SYDNEY SMITH, *Demonstrator of Physiology at St Mungo's College, Glasgow.*

SOME little time ago, in the preparation of specimens for the practical class in Physiology at St Mungo's College, I noticed that a ribbon of sections of a foetus which had been floated out on hot water and left over was faintly stained in parts owing to the presence of an accidental drop or two of methyl-violet in the water.

I found that the parts stained were cartilage, the obvious suggestion being that the paraffin had not penetrated the cartilage. I thought the idea of staining in the paraffin worth following up, and since then have obtained very gratifying results with all tissues and all stains so far experimented with.

The following method gave the best results :—

1st. The tissues were embedded and cut with a rocking microtome in the ordinary manner.

2nd. The sections were placed in ribbons on the desired stain in a flat vessel, care being taken to leave room for the specimens to straighten out.

3rd. The vessel was covered to limit evaporation and keep dust out, and left in a warm place until the sections were perfectly flat, when it was transferred to an ordinary temperature. The stain was allowed to act for, on an average, from twelve to twenty-four hours, according to the penetrating power of the stain used.

4th. The staining fluid was poured off slowly, so that the sections were left lying at the bottom of the vessel, just as a ribbon is left on a slide in mounting by the hot-water method.

5th. Water was slowly added, the ribbons floated up, and the loose stain thoroughly washed from the under surfaces of the sections. If the sections were over-stained, the excess was removed by the ordinary methods.

6th. The sections were then mounted on slides, allowed to dry, passed through turpentine or xylol to remove the paraffin, and mounted in Canada balsam.

If it is not convenient to wait for the sections to dry, the water may, of course, be removed by alcohol, and then, as before, through turpentine to Canada balsam. Up to the present time good results have not been obtained with much less than twelve hours, with most of the stains. Direct, indirect, and double stains appear to work equally well. An advantage of this method seems to lie in the fact that it is possible to give thin specimens to the students to stain, without any great risk of breaking them in the process, as the paraffin holds the parts together, though the time required for the stain to act is certainly a drawback. This difficulty may be over-

come by giving out the specimens at the meeting of the class previous to the one on which they are required, and allowing them to lie on the stain during the interval.

There is something also to be said for the simplicity and general efficiency of the method, and the absence of alcohol is a very important item where many students are concerned. Presumably, the reason perfectly embedded tissues will stain in the paraffin is, that individual cells are cut through and left on each side of the section with, as it were, a raw surface, the cells being held in position by lines or fences of paraffin. I have reason to believe that the principle of the method has been followed by other workers, but there are details of considerable importance in its practical application, as described in this note.

# Journal of Anatomy and Physiology.

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THE STOMACH AND PYLORUS.<sup>1</sup> By RICHARD J. A. BERRY, M.D., F.R.S. Edin., *Lecturer on Anatomy, School of Medicine of the Royal Colleges, Edinburgh*; and JOHN CRAWFORD, M.B., C.M. Edin. (PLATES XXIII.-XXVI.)

(From the Laboratory of the Royal College of Physicians, Edinburgh.)

THE present paper is the result of an investigation which was primarily undertaken with a view to determining the actual movements of the stomach during the process of distension. As the work proceeded it soon became manifest that the results were gradually diverging along three different paths: first, the relative proportions of the stomach, and the shape and dimensions of the pylorus; second, the movements of the stomach during a process of experimental distension; and third, the topographical anatomy of the stomach. The present paper deals with the first only of these three fields of research.

As our object was not the estimation of the actual size and dimensions of the stomach *in situ*, but rather the elucidation of the relative proportions of the various parts of the viscus one to another, it was considered advisable in every instance to remove the stomach from the body. After removal it became imperative to place each stomach in precisely the same condition. This end was achieved by completely distending each one with air, and allowing the viscus to dry in this condition. It is, of course, obvious that removal of the stomach from the body cannot serve as any criterion of the actual size of that organ, but it is equally obvious that under the same conditions the relative proportions of one part of the stomach to another will always remain the same, hence the course adopted. The ob-

<sup>1</sup> Read at the April meeting of the Anatomical Society.

servations which result are based on an examination of fifty stomachs, and in every instance the measurements were most carefully estimated by an instrument specially designed for the purpose.

### I. *The Relative Length of the Greater and Lesser Curvatures.*

In the last edition of *Quain* it is stated that "the great curvature is four or five times as long as the small." This statement is not borne out by our experience. In our series of cases the relative proportion of the length of the greater curvature to that of the lesser curvature was as 1000 is to 310, that is, speaking generally, as 3 is to 1. We should, then, rather prefer to state that the greater curvature is three times as long as the lesser. In only one case was the proportion 4 to 1, and that occurred in a female aged 62, where the actual measurements were (stomach fully extended), lesser curvature 13.3 cm., greater curvature 58.0 cm. There seems to be no doubt that the disparity between the two curvatures is more marked in the female than in the male; for whilst the proportion given above of 1000 to 310 may be taken as the average, we found that in the female the proportion was as 1000 is to 299, and in the male as 1000 is to 315.

### II. *The Length and Breadth of the Stomach.*

Speaking of the dimensions of the stomach, it has been stated that "when moderately filled, its length, measured from the top of the fundus to the lowest part of the great curvature, is about 10 or 12 inches, and its diameter at the widest part from 4 to 5 inches." Subject to reservations, our observations confirm this statement. We should rather say that under the fullest distension, not "when moderately filled," the length is 27.8 cm. and the breadth 13.1 cm.; that is, about 11 inches by 5. We are strongly of opinion that such dimensions are purely post-mortem, and that during life the stomach never attains anything like such dimensions, except as a result of pathological conditions.

### III. *The Relative Proportions of the Antero-Posterior and Transverse Diameters of the Stomach.*

On examining the proportions of these two diameters, we were at once struck by the fact that the distended stomach is always broader from side to side than from before backwards. To this there was not a single exception in the entire series, not even in those younger persons in whom the liver is relatively larger. The actual ratio of the transverse diameter to the antero-posterior we found to be as 1000 is to 930. In the female the two diameters are, however, more nearly equal, the exact ratio being as 1000 is to 952, whilst in the male it was as 1000 is to 922. The greatest difference between the two diameters occurred in a male aged 22, where the actual measurements were, transverse 14.2 cm., antero-posterior 12.0 cm., giving a ratio of 1000 to 845. The least difference also occurred in a male aged 33, where the diameters were so nearly equal as to give a proportion of 1000 to 985.

### IV. *The Relative Proportions of the Vertical Length of the Stomach to the Transverse Diameter.*

Our observations have shown us that the length of the stomach bears certain very definite relations to its transverse diameter, the exact ratio being as 1000 is to 463. In the female the disparity is even greater, with a proportion of 1000 to 430, whilst in the male the difference is not so marked, being only as 1000 is to 480. In other words it may be stated that on an average the length of the stomach is about two and a quarter times greater than its transverse diameter; in the female rather more so, in the male rather less so.

### V. *The Influence of Age and Sex on the Dimensions of the Stomach.*

If the foregoing ratios have been carefully observed, it will be obvious that sex has a slight but important influence on the shape and dimensions of the stomach. It has been noted that in the female the disparity between the greater and lesser curvatures is more marked than in the male; the disparity

between the antero-posterior and the transverse diameters is less marked than in the male; whilst, lastly, the length of the stomach in the female exceeds the transverse diameter in a relatively greater degree than in the male, consequently the female stomach is longer and more nearly tubular than in the male.

Age, so far as we can ascertain, has no appreciable relative influence on the dimensions of the stomach. In our series of cases the relative dimensions of the stomach were very constant at all periods of life, but were smallest between the ages of 20 and 30. Whether this is to be taken as indicating that the functions of the stomach are temporarily lessened concurrently with the cessation of growth, we cannot say. If age has any appreciable influence on the dimensions of the stomach, we are of opinion that a very large number of observations will be required to elucidate the fact.

#### VI. *The Cardia.*

The cardiac orifice in the completely distended stomach, as seen from within, is usually somewhat funnel-shaped. Its dimensions are very variable, and have not, so far as we can ascertain, any ratio to either sex or age. In the ordinary textbook description of the cardiac orifice no mention is made of a cardiac valve; it is apparently assumed to be non-existent, yet such is not the case. A crescentic valve is very frequently found, situated most usually at the upper and back part of the orifice, and projecting downwards, with a depth varying from two to five millimetres. Such a valve we found to be present in about 50 per cent. of cases, and rather more frequently in the female than in the male; but we are of opinion that if the mucous membrane be examined in a fresh condition, this valve will be found to be almost constantly present. We are further of opinion that this valve, small though it be, is an actually functional valve. The reasons which have led us to this belief are, briefly, as follows: the termination of the œsophagus opens obliquely into the stomach, and during digestion its walls are in contact; the actual cardiac orifice will thus be a mere slit, so that a valve two millimetres in depth is more than sufficient to obliterate such an aperture. Further, the valve being suspended, as it is, from



above, acts somewhat like a swing door opening both ways. Under ordinary conditions it merely shuts off the œsophagus; but given the formation of gas during digestion, this may swing the valve towards the œsophagus, and so escape *per oram* as an eructation; similarly with vomiting, the abnormally violent muscular contractions easily overcome the resistance of the valve, thus permitting of regurgitation of the stomach's contents. Lastly, this view would appear to be confirmed by certain experiments which we have been conducting, and to which we hope to refer in a subsequent paper.

### VII. *The Pylorus.*

With regard to the shape of the Pylorus, we find it stated in *Quain* that "internally its opening is usually circular"; and further on, that "occasionally the orifice is oval, and it is often placed a little to one side." Dwight, on the other hand, says: "Though it is understood that its opening may be oval, it is generally described as circular. . . . The following table of 30 observations on casts shows that it is practically always oval." Our own observations support those of Dwight. In nearly 70 per cent. of our cases the pylorus was distinctly oval, having average diameters of 18 millimetres by 14 millimetres. Though the remaining 30 per cent. of our cases were classified by us as circular, it must be remembered that the shape in these cases was determined by the eye alone, so that we are very strongly of opinion that Dwight is correct when he says "it is practically always oval." As regards the actual size of the orifice in Dwight's 30 cases, the average dimensions were rather less than in our 50 cases, Dwight giving  $14 \times 11$  millimetres, as opposed to our  $18 \times 14$  millimetres. Speaking of the direction of the longest axis of the oval, Dwight says that he has been unable to ascertain any definite direction. With this we cannot altogether agree; for, whilst admitting that the direction is variable, we found that in nearly 70 per cent. the direction was obliquely from above, downwards and backwards. This direction, then, we regard as the more or less normal one. Other directions that we found were vertical, and horizontal from before backwards.

Huschke has been quoted as saying that "sometimes the

circular rim is imperfect, and there are found instead two crescentic folds, placed one above the other, below the passage; and lastly, there is occasionally but one such crescentic fold." The former condition we did not meet with, and the latter only twice. With regard to the single crescentic fold, it is obvious that such a condition results from the actual orifice having been placed rather near the periphery than usual.

Another condition which we did find on several occasions has not, so far as we are aware, been previously described. It is the occurrence of a second and even a third crescentic valve in addition to the pyloric valve proper. A second crescentic valve we found in 14 per cent. of our cases, and a third valve in 2 per cent. When the second valve does occur, it appears to be usually crescentic and somewhat variably situated. The additional valve occurred rather more frequently in the male than in the female.

#### CONCLUSIONS.

1. The greater curvature is usually three times as long as the lesser curvature,—not four or five.
2. The transverse diameter of the stomach is always greater than its antero-posterior diameter.
3. The length of the stomach is about two and a quarter times greater than its transverse diameter.
4. Sex has an appreciable influence on the shape and dimensions of the stomach, the female stomach differing from the male in its relatively greater length, in being more nearly tubular, and in the greater disparity between the two curvatures.
5. There is frequently a cardiac valve, which the authors believe to be functional.
6. The pylorus is oval, not circular, in outline, and its longest axis is most frequently directed from above, downwards and backwards.

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Dr BERRY on the Stomach and Pylorus.



FIG. 1.—To illustrate the cardiac valve of the stomach.

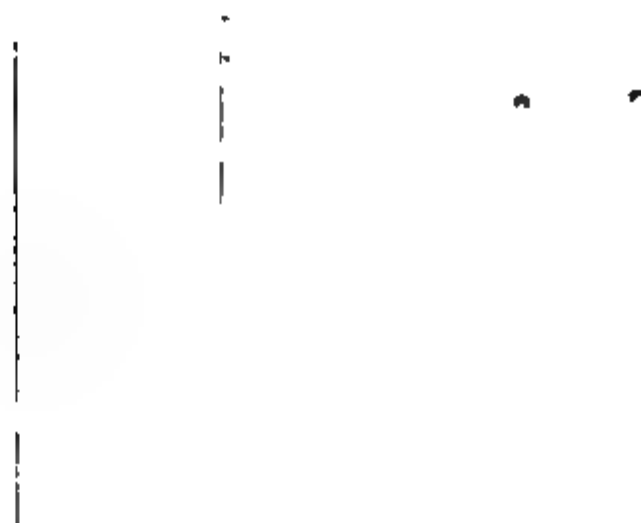
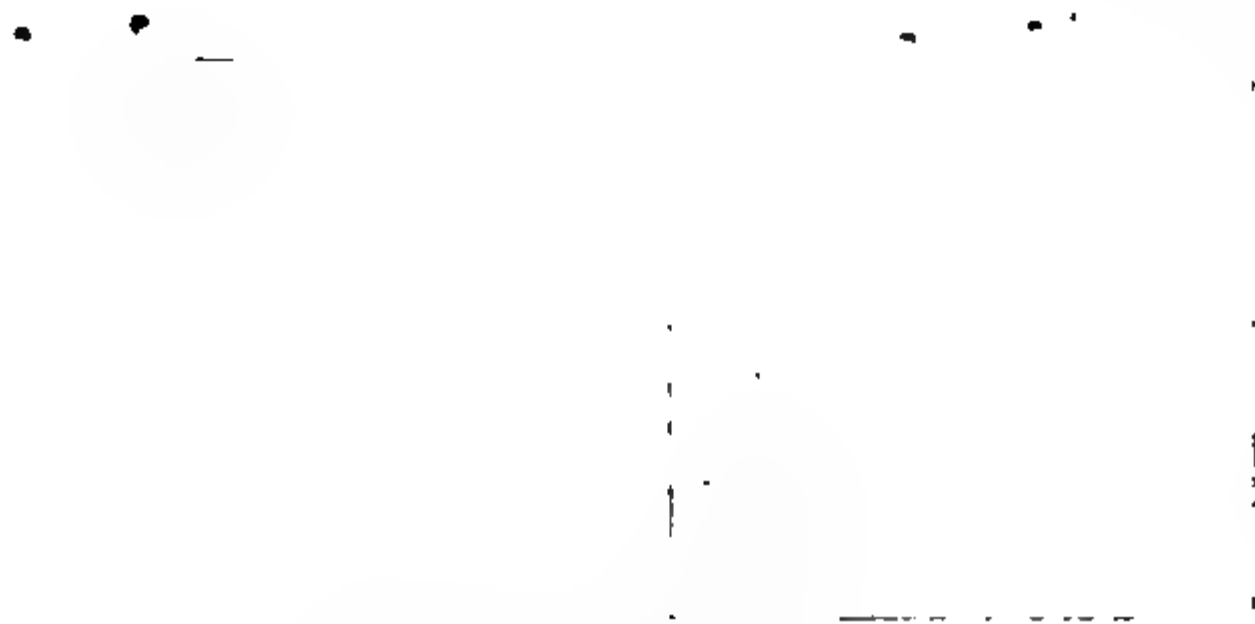


FIG. 2.—To illustrate the cardiac valve of the stomach.



**FIG. 3.**—To illustrate the oval pylorus with its longest axis directed from above, downwards and backwards.

**FIG. 4.**—To illustrate the pyloric orifice with an irregularly circular orifice.





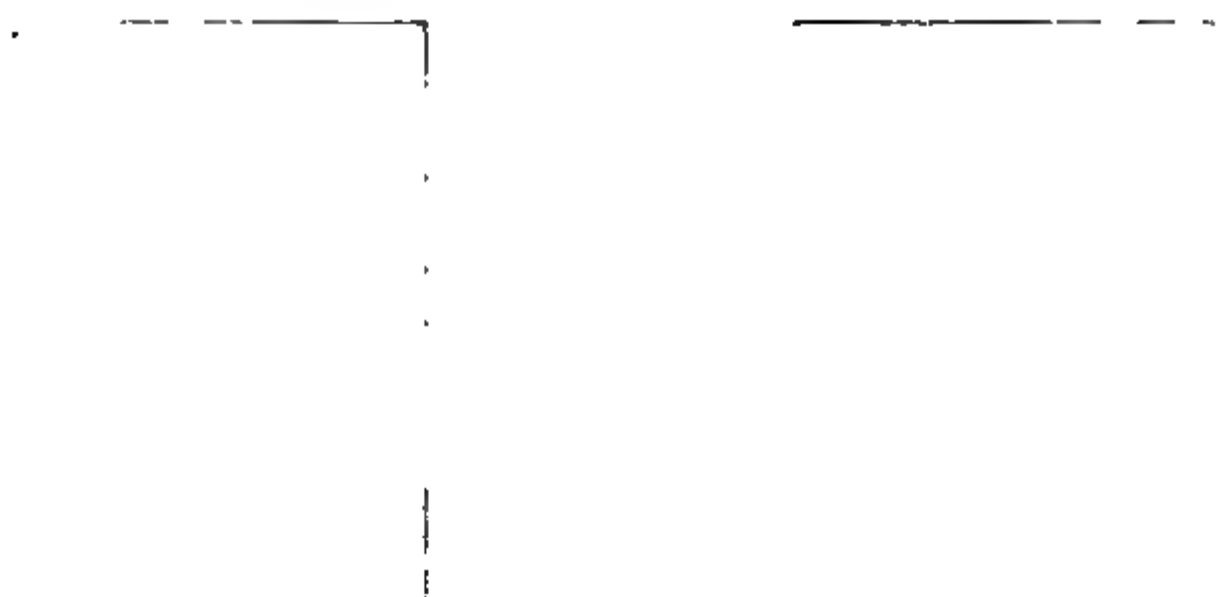


FIG. 5.—To illustrate a pyloric orifice with a single crescentic valve.

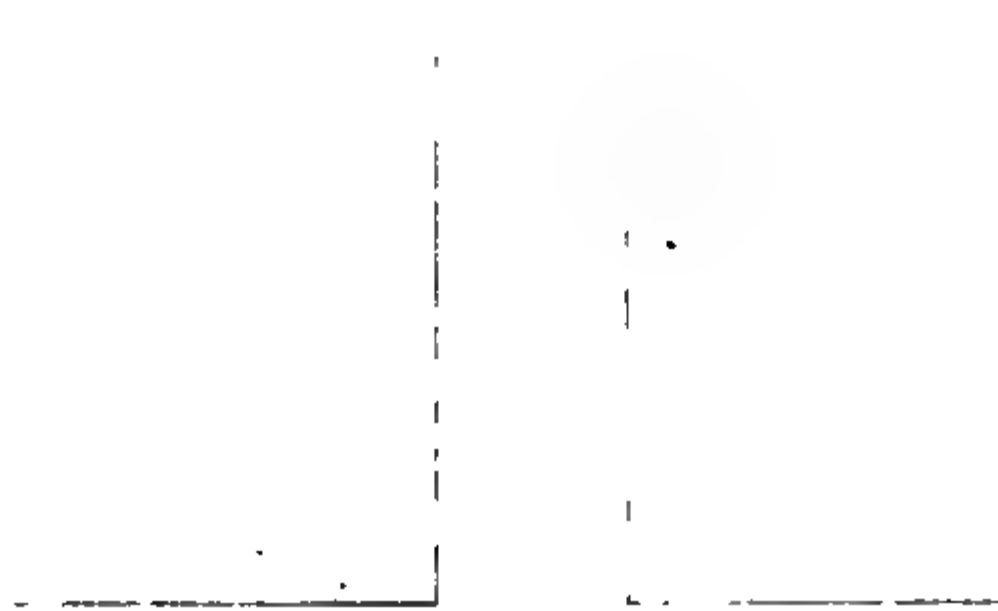


FIG. 6.—To illustrate a pyloric orifice with a second crescentic valve.





FIG. 7.—To illustrate a pyloric orifice with a second crescentic valve.

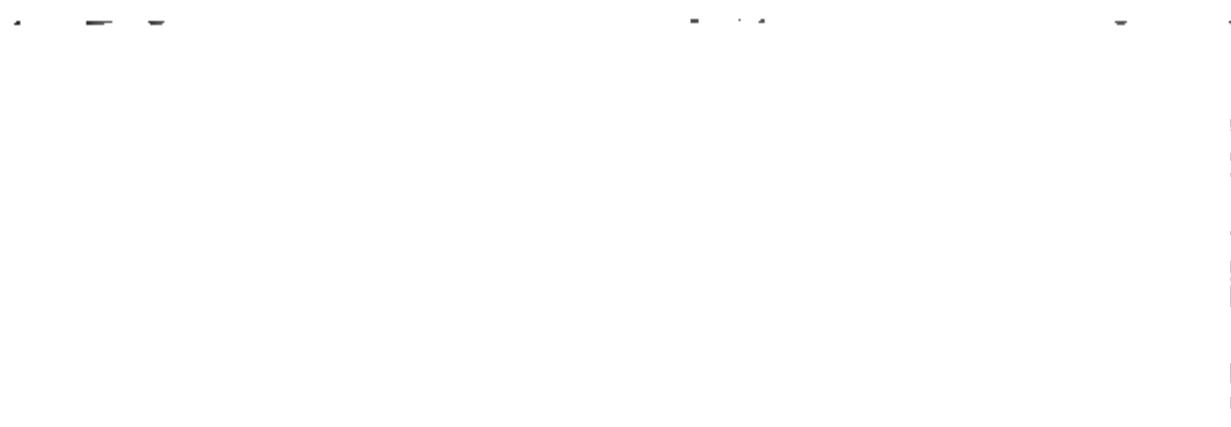


FIG. 8.—To illustrate a pyloric orifice with a second crescentic valve,  
and with traces of a third valve.



DUPLICITY OF CERVIX UTERI IN TRICHECUS AND  
OTARIA. By Professor CLELAND, F.R.S., Glasgow.  
(PLATE XXVII.)

HAVING had occasion to make some preparations from a young female walrus about five feet in length, presented to me by Mr Bostock, I was astonished, on examining its genito-urinary organs, to find that the uterus was internally completely double, as in the monotremata. True, there was a well elongated vagina and a cervix uteri, whose extremity projected into it; but this projection exhibited two orifices placed close together, each of which led into a distinct uterus divided into cervix and cornu.

I felt puzzled to know if by some chance it had happened that this particular specimen exhibited a remarkable example of that bicornute anomaly which is occasionally met with in the human subject, or if this extraordinary condition was really the normal arrangement in the walrus. I had no means of getting another specimen for comparison. But while the difficulty was still occupying my thoughts I happened to lay hands on the uterus of a sea-lion (*Otaria jubata*), which had been laid aside till I should find time to prepare it for exhibition as a jar specimen, and for which I had also been indebted to Mr Bostock's kind thoughtfulness for science. It at once occurred to me that this might possibly show something throwing light on the uterus of the walrus.

I proceeded accordingly to examine the interior. At first I was disappointed. The os uteri externum showed only one opening, and the cavity of one of the cornua was traced down to the place of junction with the other cornu, and thence continuously to the os. But happily there was noticed a curious irregularity of the rugæ on the side corresponding with the other cornu, and on closer inspection it was found that there were two passages in the upper three-fourths of the cervix, that the septum between the two was of no great thickness, that

there depended from its retroserial or vaginal edge a short uvular process reaching almost to the external os, and that it ended in an edge proserially in such a position as to leave a communication between the two cornua of sufficient size for the passage of a goose-quill.

I took the precaution of re-examining the uterus of the seal (*Phoca vitulina*), and was soon assured that it presented not the slightest trace of inclination to persistent duplicity of the Müllerian duct, retroserial to the point where the cornua uteri separate. The overwhelming probability is that the conditions seen in the walrus and sea-lion are normal. It seemed, indeed, at first possible that the one example of walrus examined presented an unusual abnormality; but assuredly it would be in the last degree unlikely for such an occurrence to be followed by a smaller degree of the same kind of abnormality in an only specimen of an allied animal. It is for other anatomists to repeat the observation of the interior of the uterus in both these animals. Meanwhile, it is simply to be noticed that the peculiarities here recorded are due to deficiency of that union of the Müllerian ducts which had been carried to its full extent in the ancestral stock, and that this failure to carry out the ancestral tendency to complete union of the oviducts from the base of the cornua to the urogenital sinus has occurred to the greater extent in the more modified of the two forms, namely, the walrus. This suggests that the consanguinity of the walrus to the sea-lion is greater than to the seal; and indeed they were already placed nearer to one another in Cuvier's *Animal Kingdom*, on account of greater resemblance of limb.

It is a long stride from any of the animals mentioned to the cetacea. But I have carefully examined the uterus and vagina of a porpoise before birth, and made certain that there is in it not the smallest trace of duplicity of the oviducts at any point posterior to the separation of the cornua uteri. It may be remembered, however, that in 1884<sup>1</sup> I placed on record that in the male white-beaked dolphin I found in the first part of the urethra, immediately beyond the openings of the vasa deferentia, "two large openings distinct one from the other, and both leading up into a single sinus pocularis."

<sup>1</sup> *Jour. Anat. and Phys.*, xviii. p. 834.

As respects other details in the anatomy of the parts in the sea-lion and walrus, it may be mentioned that, in both, the specimens the cervix uteri is about an inch long, and that, in both, the mucous membrane of the cervix, as well as the rest of the uterus, is longitudinally rugose, the rugæ of cervix and cornua being continuous at the os internum, but presenting at that part a momentary constriction of each ruga, so as to make a circular indentation crossing the series. The cornua of both specimens are dilated in the middle and semicircular in curve, ending abruptly in a Fallopian tube, which arises in the wall of a peritoneal hood furnished with only a small orifice placed close to the end of the cornu. This orifice is smaller in the sea-lion than in the walrus. In both there is a vascular fringe close to the orifice of the sac, in connection with the extremity of the Fallopian tube; but it is best developed and most laminated in the sea-lion. In both specimens the urethra is elongated, and the urethral orifice is in connection with a hymeneal fold. In the walrus the hymeneal fold is simple, and the urethral orifice three inches removed from the truncated glans clitoridis, which lies in a preputial depression close to the outside. In the sea-lion the glans clitoridis, together with the largely developed clitoris, is similar to that of the walrus; but the urethral orifice is not more than an inch and a half from the glans clitoridis, and the hymeneal fold retreats dorsally from the vulva, and presents dorsally about half a dozen well marked pointed processes continuous with as many longitudinal rugæ of the vagina.

As I have had occasion to mention a dissection of a foetal porpoise, I may note that in it the urethra is close to the clitoris; there is thus no deep urogenital sinus; also there is no hymen. But the vagina is enormously elongated, and is divided into a straight vulvar or superficial portion, and a deep part crumpled up and separated from the superficial part by a constriction. The cornua uteri have the mucous membrane coarsely rugose, while the cavity of the cervix and the vaginal aspect of the os externum present a much finer longitudinally rugose appearance.

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EXPLANATION OF PLATE XXVII.

Fig. 1. *Trichecus rosmarus*.—*a*, Ovary laid bare by cutting open the peritoneal hood; *b*, the opening of the hood; *c*, round ligament of uterus; *d*, cornua uteri laid open; *e*, cervix uteri; *f*, os uteri; *g*, vagina; *h*, urethral orifice; *i*, interior of urogenital sinus; *k*, elevation caused by body of clitoris.

Fig. 2. *Otaria jubata*.—*a*, Highly complex and vascular fimbriæ tubæ; *h*, portion of uterine wall to which the septum partially dividing the cervix is attached; *i*, uvular extremity of septum. The other letters are the same as in fig. 1.

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J Cleland del

F Heath, Lith<sup>r</sup> Edin<sup>r</sup>

CERVIX UTERI IN TRICHECUS & OTARIA.





ON THE VITALITY OF THE OVA AND SPERMATOOZOA  
OF CERTAIN ANIMALS. By JAMES F. GEMMILL, M.A.,  
M.B., *Lecturer on Embryology, and Assistant to the Professor  
of Anatomy, Glasgow University.*

THE ripe sexual products of many marine animals are shed into the sea-water, and, apart from the attraction which ova exercise on spermatozoa within short distances, the meeting of the two elements in fertilisation depends in great part on accidental causes. No doubt considerable waste of material takes place. It is by no means rare to find unfertilised ova in tow nettings. To provide for the fertilisation of even a moderate number of eggs a greater amount of sperm must be produced by the male than in cases where the contact of ovum and sperm is artificially aided.

Many echinoderms and molluscs breed under the conditions above described. The sea-urchin, *Echinus sphaera*, and the limpet, *Patella vulgata*, may be taken as typical examples, the former being ripe in April on our coasts and the latter in October.

Considerable interest will centre round any facts that can be made out regarding the duration of vitality of the ova and spermatozoa of these animals under normal conditions. In the case of spermatozoa, a further question will present itself, viz., how far and at what rate do they travel by their own movement, and from what distances are they attracted by ova?

DURATION OF VITALITY OF SEA-URCHIN EGGS IN SEA-WATER.

In carrying out each set of observations on this point fresh ova were shed into a series of vessels containing sea-water. Then at short intervals some freshly-obtained sperm was shed into the vessels successively. After a sufficient lapse of time the results of each attempted fertilisation were noted under the

microscope, attention being paid to the segmentation and general development of the ova, and to the proportion in numbers between the unsegmented ova and the normal and abnormal morulae and blastulae.

While, on the whole, the results of different experiments were fairly uniform, still variations occurred from time to time, due no doubt to differences in the ripeness and general condition of the ova and sperm available. On an average, it was found that when ova have been shed for from one to four hours, they are in the best state for normal fertilisation, and give rise to few cases of polyspermy and irregular development. Up to nine hours there is little loss of vitality. Weakness, however, now begins to make its appearance, and goes on increasing with each interval. After seventeen hours a very considerable number of ova are quite incapable of fertilisation, or develop abnormally. With each succeeding hour this number increases rapidly, until after from twenty to twenty-four hours only 1 or 2 per cent. of actually living ova remain. In no case was segmentation observed in ova that had been shed for twenty-eight hours or more.

From this it appears that the life of an unfertilised sea-urchin egg in sea-water is comparatively short. The limit of probability in its favour is little over half a day, while the limit of possibility is practically fixed at twenty-four hours.

It is a remarkable fact that polyspermy and irregular development are more apt to occur in the case of ova that are fertilised immediately after being shed into sea-water than in those which have been left to themselves for a little, *e.g.*, for from one to four hours before fertilisation is attempted. Apparently the short interval gives them time to round off their circumference, and allows their peripheral layer to become accustomed to the medium of sea-water. One finds under the microscope that many ova which are at first irregular in outline by-and-by round themselves off into perfect spheres. As is well known, in the normal fertilisation of the sea-urchin egg, immediately after the entrance of the first spermatozoon head, the peripheral layer of the ovum throws off a delicate but firm membrane—"the membrane of fertilisation"—which effectually prevents the entrance of additional spermatozoa. In well-marked cases

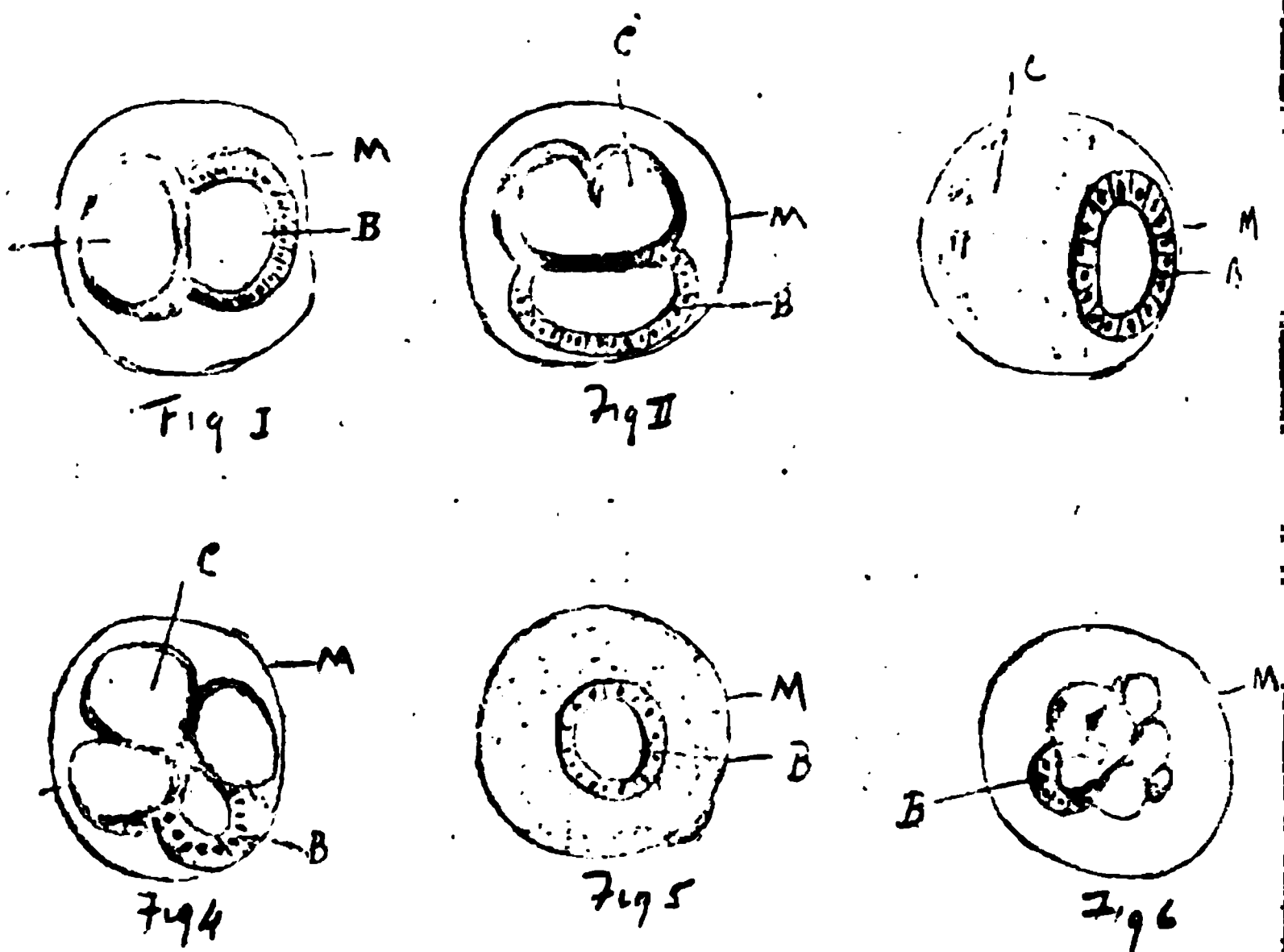
of polyspermy this membrane is never formed. It is to be noted, however, that when perfectly fresh ova are taken from urchins that are perfectly ripe, immediate fertilisation may be effected without the occurrence of more than occasional cases of polyspermy. But whenever the ova are taken from a gland that is either immature or half spent, more cases of polyspermy occur with immediate than with delayed fertilisation.

No doubt polyspermy may occur also from general lowering of the vitality of the whole ovum. Whenever the sea-urchins used, whether ripe or not, were not quite fresh—*e.g.*, when they had been kept in stagnant sea-water, or had been out of the water altogether, either in the laboratory or on the shore above low-tide level, the number of cases of polyspermy on immediate fertilisation was relatively very great. In one extreme instance, where the sea-urchin from which ova were taken had been kept in the laboratory among damp sea-weed for thirteen hours, not a single case of normal development resulted in the set to which spermatozoa were immediately added; while out of another set of the same ova, which was allowed to remain in sea-water for four hours before the addition of spermatozoa, 75 per cent. of normal blastulæ resulted. Probably when first shed the ova in question were in a state of semi-asphyxia, from which they gradually recovered when allowed free breathing space in the sea-water.

As before stated, considerable variations occur in the duration of vitality of ova taken from different sea-urchins, and apparently the origin of these variations, other things being equal, is to be found in the comparative spentness of the urchins. In proportion as the glands are exhausted, and according as they reach the extreme of exhaustion, the shorter is the term of free life in the ova obtained from them. They may even be incapable of fertilisation after so short a period as five hours. In such cases, also, at all intervals, great numbers of examples of abnormal development occur. Among the commonest and most easily recognised are such malformations as the formation of a rosette of small, incompletely-separated cells at one end, unequal total segmentation, complete and incomplete blastulæ of half, quarter, or one-eighth the normal size, blastulæ of full size without a proper blastocœle, etc. A few drawings are

given below, taken from the results of a fertilisation made on 17th May 1898. The duration of vitality of the unfertilised ova in this set was not greater than seven hours.

One can always count on getting a great number of abnormalities from the ova of spent urchins. The most of these are of the incomplete type—*e.g.*, hemiblastulæ derived from one of a two, four, or eight celled stage (figs. 2, 4, 6). Less common are forms such as are indicated in figs. 3, 5, where the blastula is complete, though not of the usual size. The cells which remain behind in development retain their form, and by their mere physical presence cause any blastula derived from a sister



Abnormalities in early development of Ova from a spent Sea-Urchin.  
(Explanation in text.)

cell to be incomplete. Similarly, in the frog's ovum, when one of the cells of a two-celled stage is killed but not disintegrated, the other will often, it is stated, develop into a hemi-embryo.

In an easy method which I have been in the habit of using in order to get abnormalities for demonstration purposes, and which consists in drawing up newly-fertilised ova into a

pipette with a very fine nozzle and then ejecting them with moderate force, one finds that complete blastulæ of smaller than normal size tend to be developed in successful experiments. Apparently the slight violence used separates the cells. It may lead to the disintegration of some of these cells, which become broken up into a mass of granular débris, and exercise no moulding influence on the development of the surviving cells.

Examples of this are seen in figs. 3 and 5. The complete blastulæ of half size seen in both have been developed from one cell in a two-celled stage. The other cell is in a state of partial or complete disintegration.

A remarkable fact noted in carrying out the experiments on the vitality of ova was that the access of spermatozoa to ova, which are moribund but not quite dead, markedly hastens their disintegration. In such cases the surface of the ova rises up into clear blister-like projections, the contents become vesiculated, and a sort of pseudo-segmentation results. Apparently the spermatozoa gain entrance, but are able to do no more than form foci of protoplasmic irritation, leading to the formation of vacuoles and to the early degeneration of the whole cell. A set of the same ova, if kept for a few hours longer (*i.e.*, till they are dead) before the sperm is added, will be quite uninfluenced by the spermatozoa, and may retain their integrity of form for days.

#### DURATION OF VITALITY OF LIMPET OVA.

Limpets are ripe during late autumn and early winter. The same routine of experiments was carried out on their ova as in the case of the sea-urchin. The term of vitality of limpet ova after being shed is somewhat longer than that of sea-urchin eggs. After seventeen hours a good culture can still in most cases be made. The usual limit is thirty hours, but in some cases it was as low as twenty-four hours, and in others it stretched out to forty. As in the sea-urchin, more examples of polyspermy and irregular development occur in ova that are fertilised immediately after being shed, than in others from the same gland whose fertilisation is delayed for an hour or two. Also polyspermy and irregular development crop up frequently

after the vitality of the ova used has been impaired by too long delay. As in *Echinus*, the influence of spermatozoa in hastening the disintegration of ova which are in a moribund condition was frequently noted.

From observations on the comparative sizes of the ovaries of a great number of sea-urchins and limpets at different times during the breeding season, it is evident that the shedding of ova takes place at intervals which are scattered over a considerable period. The whole contents of the glands are not emitted at one time, but only the ripest part. The actual process of shedding was only observed in the sea-urchin. In two cases which came very directly under observation, the animals had been kept isolated in captivity in small tanks, and when the process began they were adherent to the sides, close under the surface of the water. The ova streamed out gently from the five genital apertures, and, the surrounding water being quite still, they showed no tendency to disperse, but fell slowly to the bottom and accumulated in a heap there. Any fluid that was poured out with the ova did not react to the sea-water by diffusion sufficiently to cause them to be scattered.

#### VITALITY OF SPERMATOZOA.

In making observations on the vitality of spermatozoa the fresh sperm of a ripe sea-urchin was shed into sea-water, and at intervals some of the mixture was added to fresh ova. After a sufficient lapse of time the condition of the ova as to fertilisation and general development was noted under the microscope. In some cases microscopic examination of the mixture of sperm and sea-water for free movement on the part of the spermatozoa was also made at intervals.

The results as to duration of vitality varied extremely, according to the amount of sperm used in proportion to the volume of sea-water into which it was shed. When a small quantity of sperm was mixed with a large quantity of sea-water, the duration of vitality of the spermatozoa is short, but when the converse proportions are used, it is greatly lengthened. This state of matters appears to be due to two

causes:—(1) Mixing with sea-water stimulates the activity of movement of the spermatozoa, which become the more active the better they are mixed with pure sea-water. Under these circumstances, their store of energy will be the sooner exhausted. (2) As spermatozoa are no doubt nourished by the spermatie fluid in which they lie, the more this fluid is diluted by the addition of sea-water the less nutritive it will become. Well developed spermatozoa may remain practically inactive inside the testes for a very considerable time. Thus for some months before the actual breeding period in most echinoderms and in the limpet, ripe spermatozoa are present in the sexual glands (along with much unripe tissue), which only need the stimulus of sea-water to make them exhibit movements. It may not be possible to obtain ripe ova from the same species for testing their fertilisation powers. But in the echinoderms it is possible sometimes to obtain ripe ova from different species, capable of cross fertilisation by the prematurely developed spermatozoa. Thus *Amphidotus cordatus* is ripe in July, but sperm taken from male specimens early in May will impregnate the ova of *Echinus sphaera* and *Echinus miliaris*.

Fully developed sperm inside the sexual gland dies rapidly if respiration is interfered with, and therefore, presumably, in normal circumstances undergoes metabolic changes and requires nutrition. While normally quiescent inside the gland, it cannot be said to be absolutely inactive. Thus in some rare cases of hermaphroditism recorded by me in the limpet,<sup>1</sup> where spermatie and ovarian tissue were both present in the same genital gland, not a few of the ova had been fertilised internally. The gland contained a considerable number of segmented ova, and of larvæ already in the trochophore stage, which began to swarm immediately after they were shed into a vessel of sea-water. It is to be noted, however, that an examination of sections of the hermaphrodite gland showed that fertilisation had taken place only in those ova which were either surrounded by spermatie tissue, or were in contact with such tissue at some part of their circumference.

<sup>1</sup> "On some Cases of Hermaphroditism in the Limpet, with Observations on the Influence of Nutrition on Sex in the Limpet," *Anatomischer Anzeiger*, Bd. xii., No. 17, 1896.

## DURATION OF VITALITY OF SEA-URCHIN SPERMATOOA.

As indicated previously, the term of vitality of spermatozoa varies according to the degree of their admixture with sea-water. Where so little spermatic fluid is used that only the slightest turbidity or milkiness results in the sea-water, the average time during which spermatozoa exhibit active movements and are capable of fertilising ova is from three to five hours. To go to the other extreme, when the mixture is so thick as to be quite milky and opaque, the vitality of the spermatozoa may be maintained for as long as seventy-two hours. By taking sperm from a sea-urchin and mixing it in different vessels with different quantities of sea-water, one obtains sets of spermatozoa which will retain their vitality for a rising series of terms, *e.g.*, 8, 12, 16, 24, 48, and 72 hours. For the longest term, the proportion of spermatic fluid to sea-water should be not less than 1 to 10.

For spermatozoa as for ova the duration of vitality varies considerably in different specimens and at different times in the breeding season. It is longest at the height of the breeding season, and becomes very markedly shortened when the animals are spent. The same strength of mixture which will keep spermatozoa alive for eight hours in the early part of April, may not serve to keep others living for more than three hours if the experiment is performed about the middle or towards the end of May. This rule holds good for all mixtures, weak as well as strong. Difference of temperature may have a slight influence in shortening the term of life of the spermatozoa during the later seasons, but even when the vessels used are kept at the temperature of the sea by being placed in a tank with circulation of freshly-pumped sea-water, the results are still substantially the same.

As regards the limpet, the general facts relating to the vitality of its spermatozoa correspond with those already given for the sea-urchin. The one difference is that the durations of vitality of corresponding strengths of mixture are greater for limpet spermatozoa. In a dilute mixture they will be active after eight to ten hours, while the limit for the sea-urchin under



similar conditions is three to five hours. It is to be noted that, as previously stated, the ova also of the limpet live longer in sea-water than those of the urchin. It is to be noted, also, that the spermatozoa of the limpet do not exhibit the extreme activity of movement shown by those of the sea-urchin.

Of observations on the vitality of other marine animals, only one example need be quoted here. It refers to a large red Nemertine which was obtained by dredging in October last, and shortly after being brought into the laboratory began to discharge streams of spermatozoa from lateral apertures at regular intervals along its body. Different quantities of the spermatozoa were put into three small vessels. The first vessel had only a small amount of sperm in a comparatively large quantity of sea-water; the second had so much sperm that its contents were milky in appearance; the third contained as thick a mixture of spermatozoa as could be obtained by means of a pipette from the dish in which the Nemertine lay. The contents of each vessel were examined from time to time under the microscope for movement on the part of the spermatozoa. The results as to activity were as follows:—

| Time of Examination.              | Dish with weak mixture.    | Dish with medium mixture. | Dish with thick mixture. |
|-----------------------------------|----------------------------|---------------------------|--------------------------|
| 8 hours after start of experiment | moderately active movement | active movement           | active movement          |
| 12     ,,                         | movement ceased            | active movement           | active movement          |
| 24     ,,                         | ... ..                     | active movement           | active movement          |
| 40     ,,                         | ... ..                     | faint movement            | active movement          |
| 48     ,,                         | ... ..                     | movement ceased           | faint movement           |
| 54     ,,                         | ... ..                     | ... ..                    | movement ceased          |

On comparing the movements of spermatozoa in different mixtures, one finds that the difference of activity is not sufficiently marked to account for the very early loss of vitality of spermatozoa in the weaker mixtures simply in terms of exhaustion of energy. I am inclined to believe that the other factor above noted, namely, the dilution of the nutritive medium by the addition of sea-water, is the more important cause. An interesting sidelight on this question is afforded by some facts which will be given later regarding the keeping alive of spermatozoa by artificial nutrition.

## MOVEMENT OF SPERMATOOA OF SEA-URCHIN.

In cases where the actual shedding of sperm was observed the urchins in question were adherent to the sides of vessels close under the surface of the water, and they emitted from their genital apertures steady streams of white sperm which, when the surrounding water was quite still, tended to take a downward curve through force of gravity. The jets, which were at their origin thin and fine, soon became expanded and cloudy by diffusion, so that by-and-by a considerable volume of the surrounding sea-water was permeated by the spermatozoa, mainly or entirely through their own activity.

The extent and rate of the movements of spermatozoa are interesting in regard to fertilisation generally, and have a special interest in cases such as those we have been considering, where impregnation takes place simply in the sea-water without connection on the part of the parents. The actual rapidity of movement of a single spermatozoon is not, however, of so much importance in this connection as the rate and extent of diffusion through a quantity of sea-water of a mass or thick mixture of active sperm. Under natural conditions the scattering of the spermatozoa will be aided by various mechanical causes, such as the action of tides, currents, waves, etc. Such mechanical factors must, however, be got rid of as far as possible in making observations on the powers of dispersion possessed by the spermatozoa themselves in virtue of their motility. Two lines of experiment were adopted in this connection: (1) to note through what distances in a mass of still sea-water (*e.g.*, in a tank or vessel) spermatozoa will disperse themselves in all directions from a definite focus; (2) to determine through what distances spermatozoa will travel in a confined space and in a definite direction, *e.g.*, along the lumen of a glass tube.

1. When a small amount of ripe sperm is introduced as gently as possible into one part of a vessel of comparatively small size (*e.g.*, 3 or 4 inches each way) containing sea-water, one finds that after some hours the sperm has diffused itself through the whole

contents of the dish, and that these have become uniformly milky. When much larger vessels are used, and all currents are avoided, the sperm does not diffuse itself beyond a certain distance from the centre of dispersion. In order to get an approximate knowledge of this distance, some shallow porcelain dishes, 20 inches long and 14 inches broad, were filled with sea-water containing fresh ova, and then left undisturbed for a time until the water was perfectly still and the ova had all settled to the bottom. Two cubic centimetres of a very thick mixture of spermatie fluid in sea-water were then, by means of a pipette, gently introduced at one corner to the bottom of each dish. The milky fluid began to spread out slowly along the bottom in a thin film, at first rather through the influence of gravity than by the activity of the spermatozoa themselves. From observations on the behaviour of spermatie fluid, the contents of which had been previously killed by gentle heat, it was judged that the influence of gravity might be counted on as causing a spread along the bottom of 3 inches (76 mm.) from the centre of dispersion. Distances beyond that were therefore considered as having been travelled over by the spermatozoa themselves by virtue of their own movements. After a sufficient lapse of time, ova were picked up by means of a fine pipette from the bottom, at measured distances from the corner in question, and were examined for segmentation changes under the microscope. By averaging the results it was found that 7 inches (177 mm.) beyond the 3-inch mark was the usual limit of dispersion. Within that limit ova were fertilised, beyond it they remained unfertilised, presumably because the spermatozoa had been unable to travel the necessary distance. To eliminate the influence of gravity, in several of the experiments a small shallow vessel was at the beginning placed in the corner of the larger vessel. The spermatie fluid was introduced into this shallow vessel, whose sides were just high enough to prevent it spreading out *en masse*, but offered no great bar to the dispersion of the spermatozoa by their own movements. The distances travelled were slightly less than in the other experiments, and were measured from the rim of the little vessel, no deduction requiring to be made for spread through gravity.

Similar experiments were carried out in a large tank,

measuring 4 feet 3 inches by 2 feet 6 inches, which was filled to a depth of 5 inches with sea-water, and allowed to remain undisturbed until its contents were quite still. Eighteen c.c. of a very thick mixture of sperm with sea-water was introduced gently by means of a syringe into a small shallow glass vessel placed at the centre of the tank. As determined afterwards by the fertilisation test, the average distance travelled by the spermatozoa in different directions measured radially from the centre was  $6\frac{1}{3}$  inches (160 mm.).

The figures given under this head and the last, while they are the actual averages of a number of experiments (eight in the former and three in the latter), should be looked upon as giving only approximate results. The experiments were carried out somewhat late in the season, and though the best available material was selected from a large number of urchins, it is possible that, had the season been less advanced, slightly longer distances might have been travelled. However, in any case, the averages given supply data for establishing fairly accurate knowledge on a subject about which, on theoretical grounds alone, one could only form the vaguest of opinions.

#### MOVEMENT OF SPERMATOOA INSIDE TUBES OF DIFFERENT DIAMETER.

Experiments such as those just described are not quite free from probable error, due to the interference of currents produced by such causes as surface evaporation, changes of temperature, etc. Then there is always a slight disturbance set up by the action of the pipette or syringe. The chance of mechanical interference will be diminished if the spermatozoa are only allowed to travel within a limited space, *e.g.*, along the cavity of a tube, and will be small in proportion as the bore of the tube is lessened.

Thin-walled glass tubes of different calibre were filled with pure sea-water, and then immersed horizontally in a mixture of sea-water and spermatozoa inside a shallow vessel placed on the stage of the microscope. It is necessary, in order to prevent through currents taking place along the tubes, to close one end

of each by a plug of some suitable substance, *e.g.*, paraffin wax. The progress of the spermatozoa inwards along the tube from the open end was watched under the microscope. One example of the results got by this method may be noted. Spermatozoa were observed to travel up a tube of  $\frac{3}{8}$  inch (2.4 mm.) in diameter for a distance of half an inch (12.6 mm.) in 7 minutes,  $1\frac{1}{4}$  inch (31.6 mm.) in 20 minutes, and  $1\frac{3}{4}$  inch (44 mm.) in 45 minutes.

Owing to the difficulty and uncertainty of detecting scattered spermatozoa under the microscope, the method of watching was given up, and a surer test, depending on the fertilisation of ova, was used. A simple way of doing this was to mix some ova in the sea-water with which the tubes were filled before their immersion in the spermatozoa bath. The tubes thus contained a number of ova at different distances from the open end, and as the tubes were left horizontal, the ova did not shift their position. The distances from the open end of those ova which were fertilised or remained unfertilised, were looked upon as giving the key to the distances travelled by the spermatozoa.

Tubes of different diameters were used, from capillary sizes upwards. The spermatozoa mixture was thick enough to be slightly milky in appearance.

In the first place, capillary lymph tubes varying in diameter from  $\frac{1}{25}$ th inch (1 mm.) to  $\frac{1}{40}$  inch (.625 mm.) were employed, and the results for these may now be given. It was found that the smaller the bore of the tube the shorter is the distance through which spermatozoa can travel along it. For capillary tubes of the larger diameter ( $\frac{1}{25}$  inch), it was noted that if the first ovum was half an inch (12.6 mm.) or less from the open end it was usually fertilised. In tubes of the smallest bore fertilisation at that distance was unusual, though it did sometimes occur. The first ovum in any of the tubes, even the smallest, did not by any means block the way against the passage of ova further up the tube, or divert them all to itself. Certainly when a large number of ova was massed near the open end of the tube, fertilisation did not occur for the usual distances beyond them, but when only a comparatively small number of ova were present in the tube, say twelve to the half inch, and especially where these were uniformly distributed, fertilisation

occurred for quite the usual distance inwards. Indeed, in not a few cases, it seemed that a succession of ova along the tube at short distances from one another attracted the spermatozoa to travel further. The longest distances recorded in this set of capillary tube experiments as having been travelled by spermatozoa, namely  $\frac{2}{3}$ ,  $\frac{2}{3}$ , and  $\frac{2}{3}$  of an inch (18.1 mm., 19 mm., 20.5 mm.), were all found in tubes which had ova placed along them at intervals of from  $\frac{1}{16}$  to  $\frac{1}{32}$  of an inch (approx. 1 mm.). With only the rarest exceptions the ova were fertilised in the order in which they succeeded each other along the tubes. Different sets of experiments give slightly different distances, but on the whole the range of variation was very limited indeed, and the results were remarkably uniform.

The method of applying the fertilisation test described above is, for various reasons, not suitable for tubes of comparatively large bore, *e.g.*, from  $\frac{3}{8}$  of an inch (2.4 mm.) onward. The following modification was used. Short glass tubes of different lengths and diameters were filled with pure sea-water containing ova. One end of each was securely plugged with cotton wool, and the tubes were then placed upright for a time in pure sea-water, until the ova inside them had all fallen down to the plugged end. They were then transferred as gently as possible to a dish containing a mixture of sea-water and spermatozoa, and immersed there, being still kept upright. After twenty-four hours the contents of each tube were poured out and examined for segmentation, etc., of the ova contained in them. Where fertilisation was present, it must have been effected by spermatozoa which had travelled down from the open end along the column of pure sea-water in the tube to the ova at its lower end. One set of measurements may be given. For tubes of  $\frac{1}{4}$  inch in diameter (6.3 mm.) all distances up to 2 inches (50 mm.) were readily passed. At  $2\frac{1}{2}$  inches (63 mm.), only a few ova were fertilised, and at  $2\frac{3}{4}$  inches (69 mm.) no fertilisation took place at all.

Another method employed of applying the fertilisation test was as follows. Two shallow vessels of equal size and shape, the one containing fresh ova, and the other fresh spermatozoa, were placed side by side, and connected by a bridge of glass tubing filled with sea-water. It was found possible to make

certain that at the start of the experiment the water inside the bridge tube should contain no spermatozoa. Before the bridge was put on, the water in the vessel containing ova was filled up to a slightly higher level than that in the vessel containing spermatozoa. Accordingly, when the bridge was set in position, a gentle current set in by siphon action from the dish with ova to the other, and this current ceased when the water in both was brought to the same level. Further currents were prevented by having the vessels of equal size and shape, so as to equalise any evaporation that might take place, and by leaving them quite undisturbed till the end of the experiment. After about twenty-four hours the ova were examined for fertilisation, which was looked upon as the test whether spermatozoa had travelled from the one dish to the other. The total length of the bridge tube was considered as the measure of the distance travelled. Other things being equal, the results varied with the diameter of the tubes experimented on, *i.e.*, the wider the bore of the tube the greater is the span of the bridge that can be crossed. For tubes of  $\frac{5}{16}$  inch diameter (7 mm. inside measurement) spermatozoa travelled along all distances up to 4 inches (100 mm.), but that is near the limit, for when tubes of  $4\frac{3}{4}$  inches (120 mm.) length were used no fertilisations resulted.

As regards the distance from which spermatozoa are attracted to ova, my results so far give little exact information. In watching under the microscope the progress of spermatozoa along capillary tubes containing ova, it was found that individual spermatozoa might travel freely past an ovum not yet fertilised without being necessarily drawn to it. On the other hand, as noted above, it was found that spermatozoa will travel further up a tube when they are led on by a series of ova at short distances (1 mm.) from each other. The capillary tubes used varied in diameter from 1 mm. to .625 mm. One may conclude, therefore, that while there is no compelling influence at .625 mm., some slight attraction does exist up to 1 mm.

The reasons why spermatozoa travel for shorter distances along tubes of small calibre will be partly physiological and partly physical. The oxygen in the water inside a small tube will readily be exhausted, and there will then be cessation of movement. But, apart from this, as the initial energy of the



spermatozoa is limited, it is to be expected (as Dr Magnus Maclean informs me) that their length of dispersion along a tube will become less as the diameter of the tube is diminished.

When the extreme differences noted above in the duration of vitality of spermatozoa in thicker and thinner mixtures were observed, and their cause referred chiefly to dilution of the nutritive spermatogenic fluid, the question was raised whether by supplying artificial food the vitality of spermatozoa, even in very thin mixtures, could not be prolonged. Some sterilised nutrient bouillon had been obtained for other purposes from Dr Ferguson of the Pathology Department, Glasgow University. The bouillon consisted of a peptonised extract in water of finely-minced lean meat. It had been carefully neutralised, and was said to contain about 40 per cent. of solids. It was first tried on the spermatozoa of a *Terebellid*. Small quantities of the spermatozoa were placed in equal proportions in four vessels containing sea-water. Two of the vessels were then left alone, a small quantity of bouillon was added to the third, and about three times that quantity to the remaining dish. The amount added to the last dish was about 4 per cent. of its total contents. On microscopic examination afterwards, it was found that the movements of the spermatozoa ceased first in the two vessels to which no bouillon had been added, but continued longest in the vessel which had received most bouillon. There was at least twenty-four hours of difference between the extremes.

This experiment has been repeated several times, and with similar results, on sea-urchin spermatozoa, microscopic examination being used to test their activity. In addition the fertilisation test was several times applied. It was found that a thin mixture of spermatozoa in sea-water to which some bouillon had been added were capable of fertilising ova for a considerably longer time than a similar set of spermatozoa to which no bouillon had been added.

One may therefore draw the conclusion that spermatozoa, when active and liberated, are capable of nourishing themselves in a suitable artificial medium, and that even in their highly-specialised ripe condition they have not given up the ordinary cell-function of nutrition. The same conclusion is



indicated by a fact that can often be observed in the routine of examining cultures, especially of limpet ova. Some of the eggs may have adherent to them cellular and other nutrient debris. In such cases it may be noted on microscopic examination of the cultures after, say, eighteen hours, that while movement has ceased in the spermatozoa dispersed throughout the sea-water, active movement is still present in the spermatozoa which have been entangled in the shreds of tissue surrounding ova.

Similarly, when any solid bits of testes have found their way into the spermatie fluid used for making cultures, these pieces, when examined under the microscope, may be found to contain active spermatozoa for a long time after all movement has ceased in the spermatozoa which are floating singly in the sea-water.

For material, laboratory facilities, etc., I have pleasure in acknowledging my indebtedness to the Committee of Management of the Millport Marine Station, and also to Mr Alex. Gray, Curator of the Station.

NOTE.—Possibly, if the habits, migrations, etc., of these animals were fully known, it might be found that the shedding of the sexual products takes place at times and under conditions which are favourable in some degree to impregnation, but so far as I know no decisive observations on this point have been recorded. It is noted at Millport that during spring and early summer urchins are found much more abundantly close inshore, both above the level of extreme low tide and just beneath it, than in the autumn and winter months. At the former season, also, they may be observed sticking to the pillars and supports of piers from which in winter they are absent. It is doubtful, however, whether this inshore migration which begins with the advent of the breeding season, is directly connected with the breeding function. Last April on examining a number of pairs of *Echinus*, which were close together on the pillars of the pier at Millport, I found that they were quite as often of the same sex as of opposite sexes. Experiments were tried on urchins collected during the breeding season to see whether the presence of ova and sperm in the sea-water stimulated male and female specimens to shed their sexual products. In some cases shed-

ding actually took place, but it also occurred with about as great relative frequency when the urchins were immersed singly in pure sea-water. The experiments were therefore inconclusive. To be decisive, they would have to be carried out on specimens that have been kept in captivity for a considerable time, and have become thoroughly acclimatised to tank-room conditions.

It is probable that the inshore migration in question has to do with feeding, seeing that in the comparatively calmer months of late spring and early summer, the ground at and near low-water mark, with its abundance of vegetable growth, will afford a rich and safe pasturage. An observation interesting in this connection has been made at Keppel Pier, Millport. Some years ago the pillars and supports of the pier gave attachment to a rich growth of algæ and hydroids, while sea-urchins were also plentiful on them in spring and early summer. Now (1898 and 1899), for some reason or other, the vegetable and hydroid growth has almost disappeared, its place being taken by great numbers of the anemone, *Actinoloba dianthus*. At the same time, very few urchins are to be found on the pier, even at those parts which are left unappropriated by the *Actinoloba*. The results of dredging just outside the pier show that urchins exist in great plenty on the ground there. This observation rather favours the view that the migration of the urchins is for feeding purposes. On the other hand, it has been noted by Mr Gray, curator of the Millport Station, and by myself, that towards the middle and end of the breeding season urchins got inshore, or near it, are less spent as a rule than those which are dredged up from deeper waters.

The limpet is sedentary for the most part, and only leaves its place for a short occasional feeding excursion when the tide is in, returning thereafter regularly to its former place of attachment. It is a very rare occurrence for a grown-up limpet to change its site. Last year a marked-off area near the middle tidal zone was carefully cleared of limpets, ninety in all being removed. Afterwards this area was carefully examined from time to time. During the first four months no new resident migrated thither, though limpets were plentiful all round about. By the sixth month the ground in

question had quite altered its character, and was covered by a thick growth of small algæ. At the same time one solitary individual of large size was found to have settled down on a corner of the area, and to have cleared off the algæ from a small surrounding patch.

The presence of ova and spermatozoa in the surrounding sea-water does not apparently stimulate male and female limpets respectively to shed their sexual products. Last October a considerable number of limpets kept in captivity at the Marine Station, Millport, were immersed singly in vessels containing fresh ova or spermatozoa. The sex and ripeness of each limpet was determined after a time by dissection. In no case was a ripe male or female found to have shed its spermatozoa or ova by the stimulation of opposite elements in the sea-water in which it was immersed.

On the whole, while further observations are needed on the breeding habits of the sea-urchin and the limpet, it is safe to say that no sexual connection takes place among these animals, and that the meeting of ovum and spermatozoon in the sea-water depends mainly on accident. In this connection two points deserve to be noted regarding their genital glands: first, the ovaries are large in proportion to the size of the animal, and produce countless numbers of comparatively small ova; second, the testes are quite equal to the ovaries in bulk, the minute size of individual spermatozoa being made up for by their vastly greater number.

THE FORM OF THE EMPTY BLADDER, AND ITS  
CONNECTIONS WITH THE PERITONEUM; TO-  
GETHER WITH A NOTE ON THE FORM OF  
THE PROSTATE.<sup>1</sup> By A. FRANCIS DIXON, M.B., Sc.D.,  
*Professor of Anatomy, University College, Cardiff.* (PLATES  
XXVIII.-XXX.)

IN a note published recently in the *Anatomischer Anzeiger*,<sup>2</sup> I have drawn attention to the fact that in specially hardened subjects, the empty bladder possesses a very definite shape or form. Since the publication of this note I have had opportunities of extending the original observations, and am now in a position to speak with more certainty of the appearances presented by the bladder, and of its peritoneal relations, as they are seen in subjects in which the various parts have been hardened *in situ*. The present description is based upon an examination of twelve subjects—ten males and two females. Nine of these were prepared by injections of strong solution of formalin; two by injections of potassium bichromate solution; while the remaining one was frozen, cut in mesial section, and the parts then thawed out in a mixture of spirit and formalin.

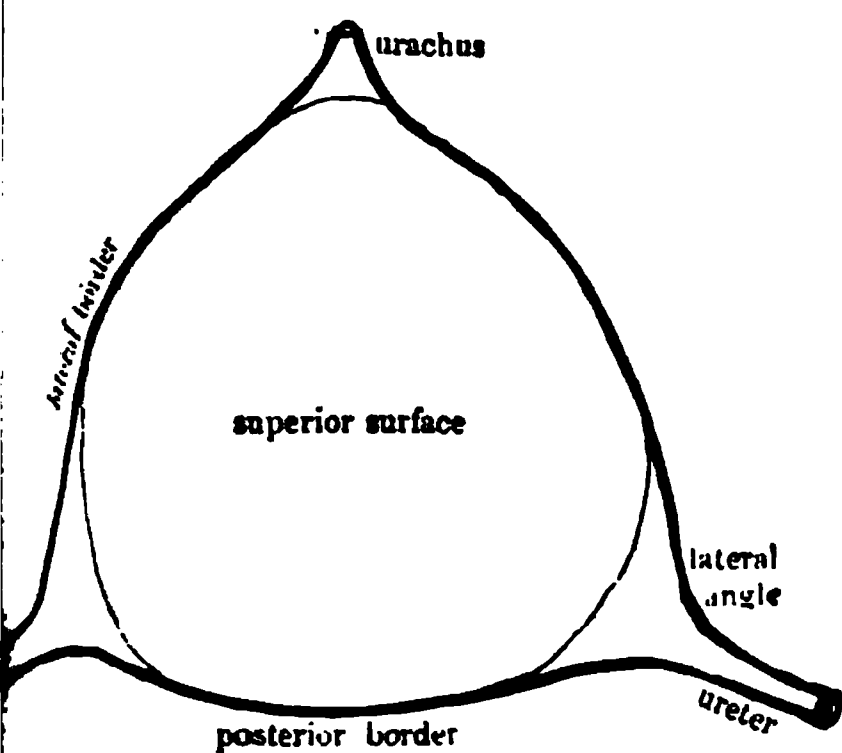
*The Empty Bladder.*<sup>3</sup>—In all the subjects except one male—in which the bladder was somewhat distended—the *superior surface* of the organ is triangular in outline. This surface is bounded on each side by a *lateral border*, extending from about the point where the corresponding ureter reaches the bladder to the bladder apex or point of attachment of the urachus; posteriorly the superior surface is limited by a *posterior border* which stretches across between the points where the two ureters reach the bladder (see fig. 1). The angle, formed on each side

<sup>1</sup> Many of the facts noted in this paper were demonstrated at a meeting of the Anatomical Society in April 1899.

<sup>2</sup> "The Form of the Empty Bladder," *Anatomischer Anzeiger*, Bd. xv., Nr. 21, 1899.

<sup>3</sup> As the passage of urine into the bladder is a continuous process, the organ is very rarely found to be absolutely empty, *i.e.*, to possess no cavity. The term, 'empty bladder,' is used in this paper to include all those cases in which the cavity of the bladder was small, its greatest vertical diameter not exceeding the thickness of the wall of the organ.

between the posterior and lateral border of the empty bladder, might be called the *lateral angle* of the organ. In subjects in which the bladder is in a contracted or systolic condition, this angle is found to correspond in position to the region where the ureter reaches the organ. When the empty bladder is not contracted, but is in the so-called 'diastolic condition,' the lateral angle may lie further from the middle line and correspond to a point above, and somewhat behind that at which the ureter reaches the bladder. Possibly this diastolic condition of the bladder is due to an abnormal relaxation of the muscular wall of the organ, as has been suggested by Anderson,<sup>1</sup> or in many cases it may be due, I believe, to an escape of fluid after death



1.—Outline of the empty bladder as seen from above.

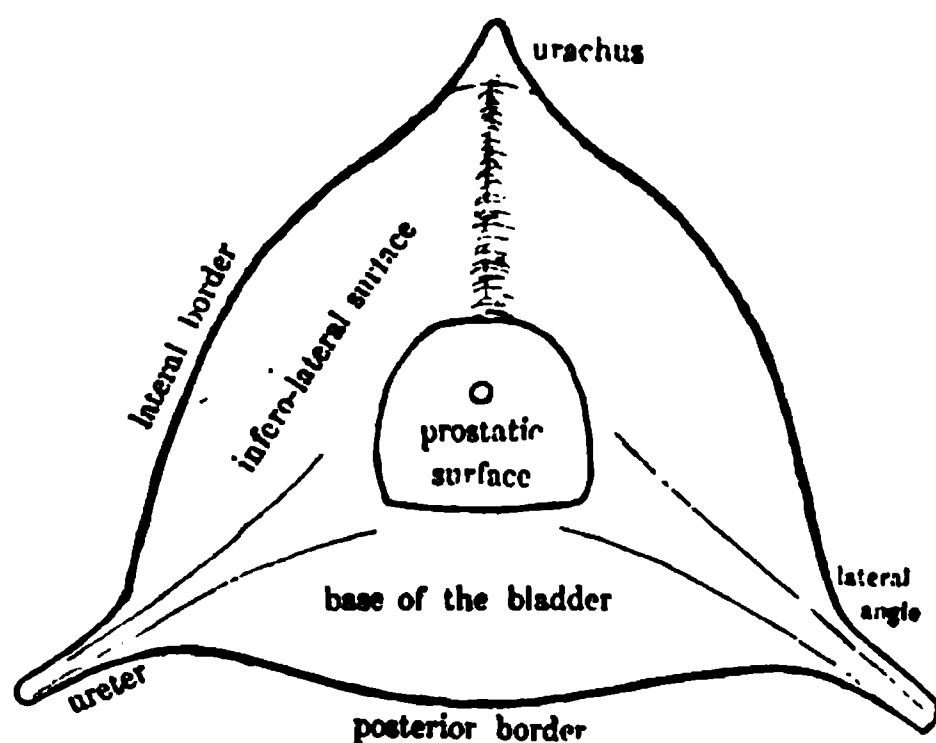


FIG. 2.—Diagram of the empty bladder as seen from below.

(at a time when the muscular wall has ceased to have the power of contracting), permitting the stretched upper surface of the organ to be pressed downwards upon the lower part of the bladder. If this is so, we must regard the appearance presented in these cases, in which the lateral angles of the empty bladder are found to lie above, behind, and a little to the outer side of the points of junction of the ureters and bladder wall, as due to post-mortem changes. In the twelve subjects which I have examined, the 'diastolic' condition was present in two cases, and in each of these the lateral angles were placed in the position just described. One of these subjects was a male, the other a

<sup>1</sup> *A Treatise on Anatomy*, edited by H. Morris. 2nd ed., 1898, p. 1016.

female. The superior surface is convex from side to side, and from before backwards, except when the organ is in the 'diastolic' condition, in which case this surface is concave.

The under aspect of the bladder is directed towards the pelvic floor, and is made up of two *infero-lateral areas*, which look for the most part downwards, outwards, and a little forwards, (resting against the side wall and floor of the pelvis), and of a part directed backwards and downwards towards the anterior wall of the rectum, from which it is separated, however, by the seminal vesicles and the terminal portions of the vasa deferentia. This latter part is the so-called *base* of the bladder. Each infero-lateral area is triangular in outline, and joins the corresponding area of the opposite side, along a rounded border which extends in the middle line from the bladder apex towards the urethral orifice. The infero-lateral area is bounded superiorly by the lateral border of the bladder, which separates it from the superior surface of the organ, while posteriorly it is separated from the basal area by a rounded border extending from the lateral angle of the bladder towards the urethral orifice (see fig. 2).

The base of the bladder is also triangular in outline, one angle lying near the urethral orifice, the others at the lateral angles of the organ. The sides of the triangle are formed by the rounded borders which extend from the lateral angles towards the urethral orifice, and by the posterior border of the organ (see fig. 2). The position of the urethral orifice on the under aspect of the bladder corresponds to the lowest part of the viscus. The opening is surrounded by a flattened area of the bladder wall, which is structurally continuous with the upper part of the prostate. The separation of the prostate from the bladder is here a purely artificial one, and must be effected by the use of a knife.

Viewed as a whole, the empty bladder might be compared to a flattened inverted tetrahedron, whose base is directed upwards, and represented by the superior surface of the bladder, while the apex, which is truncated, is directed downwards, and corresponds to the position of the urethral orifice. The three basal angles of the tetrahedron are represented by the bladder apex and the two lateral angles of the organ.

It is interesting to notice that the shape of the bladder in the human embryo of 11.5 mm., as shown in the models of Keibel,<sup>1</sup> in many ways closely resembles that just described for the empty organ of the adult. Model No. 4 of Keibel's series shows that the developing bladder possesses surfaces corresponding to the superior, basal and infero-lateral areas of the adult. The lateral angles, the anterior angle (or bladder apex), and the inferior angle or point where the developing urethra leaves the bladder, are also to be recognised at this time. The resemblance between the shapes of embryonic and adult organ is, however, soon lost during the course of development.<sup>2</sup>

There can be little doubt that the contracted bladder takes the tetrahedral form just described owing to the fact that the four points where the two ureters, the urachus and the urethra, join the organ are more firmly fixed in position than other parts of the bladder wall. As the organ contracts upon itself during micturition, these four points are more or less held apart, and so become the four angles of a tetrahedron.

#### COMPARISON WITH SOME OTHER DESCRIPTIONS OF THE EMPTY BLADDER.

Many of the published descriptions of the empty bladder are evidently based upon an examination of mesial sections through the pelvis. Symington,<sup>3</sup> for instance, states that "the empty diastolic bladder has three surfaces—a *superior*, with its concave upper aspect covered by peritoneum; an *anterior*, lying above the pubo-prostatic ligaments, and behind the pubic symphysis, and a *posterior*, which is in relation with the rectum, vasa deferentia, and seminal vesicles in the male, and the cervix of the uterus and upper part of the vagina in the female." In this description the greater part of the under surface corresponding to the infero-lateral areas mentioned above receives no

<sup>1</sup> "Zur Entwicklungsgeschichte des Menschlichen Urogenitalapparates," *Archiv. für Anat. u. Entwicklungsgeschichte*, 1896, Taf. iii. fig. 6., and Models by F. Ziegler, Nos. 4 and 5.

<sup>2</sup> See Keibel's Model, No. 7, and also the condition at birth, fig. 6 of this paper.

<sup>3</sup> *Quain's Anatomy*, vol. iii. pt. iv., 1896, p. 206.

notice. The term *antero-inferior* or *pubic surface* is used by Symington<sup>1</sup> in another place to indicate that part of the bladder wall which is formed by the meeting of the right and left infero-lateral areas described above. Inasmuch as these infero-lateral areas extend backwards as far as the lateral angles of the bladder, it would be inexpedient to apply the term 'anterior' or 'antero-inferior' to them collectively. Symington states that "the *sides* of the bladder, when this organ is empty, are very narrow"<sup>2</sup>—the narrow sides here noted will correspond with the lateral borders mentioned above.

Cunningham<sup>3</sup> describes the empty bladder as possessing *superior, basal, and inferior walls*; by inferior surface he seems to indicate only the part of the wall which lies between the urethral orifice and the bladder apex.

Anderson<sup>4</sup> states that "the form of the empty bladder is still doubtful, as appearances in the dead subject do not necessarily coincide with the condition existing during life." He considers that the 'diastolic' form is probably "not altogether the normal result of relaxation preliminary to refilling, and that the healthy living bladder retains a rounded or ovoid form even when empty."

Cleland and Mackay<sup>5</sup> describe the 'lateral edges' of the empty relaxed bladder, and apply the terms 'posterior' and 'anterior' to the two surfaces of the organ which meet at these edges. These 'posterior' and 'anterior' surfaces correspond to the superior and infero-lateral surfaces described at the beginning of this paper. The authors state that not only do the lateral "edges disappear as the organ becomes rounded out," but that "in like manner the edges disappear when the organ is drawn together in full contraction." In the specimens which I have examined the lateral borders were distinct even when the bladder was fully contracted; they are, however, naturally most sharply defined in the empty 'diastolic condition.'

Waldeyer<sup>6</sup> states that the empty male bladder is egg-shaped

<sup>1</sup> *Loc. cit.*, p. 208.

<sup>2</sup> *Loc. cit.*, p. 209.

<sup>3</sup> *Manual of Practical Anatomy*, vol. i. p. 571.

<sup>4</sup> *A Treatise of Anatomy*, edited by Morris, 1898, p. 1016.

<sup>5</sup> *Human Anatomy*, 1896, p. 768.

<sup>6</sup> *Das Becken*, 1899, p. 287.



and flattened from before backwards. The narrow end of the organ is directed upwards, the broader one downwards. Among variations he notes that the empty bladder is rarely spherical, more often pear-shaped, while sometimes the tubular condition of the child's bladder is retained in the adult. Waldeyer distinguishes in the empty bladder an *anterior* and a *posterior surface* (facies anterior and f. posterior) and a *base* or *fundus*. The *lateral margins*, which are described as rounded, are also noticed. The 'posterior surface' represents the surface described as superior in this paper, and the 'anterior surface' is represented by the two infero-lateral areas. The portion of the bladder which is fused with the prostate is stated to be really a portion of the *fundus*, but it receives the special name of *neck* (collum vesicæ). Waldeyer<sup>1</sup> mentions that under certain conditions a sharply marked angle (Blasenwinkel) is to be observed between the upper and posterior walls of the empty, or partially distended, bladder, and several of the ~~medial~~ sections figured by him show this condition. The figures show that this 'Blasenwinkel' corresponds to the line of the posterior border of the empty bladder which, as described above, stretches across between the lateral angles of the organ. The angle is seen in figs. 8 and 9 of this paper. According to Waldeyer, the angle is more common in the female than in the male. The dish-shaped form (Schüsselgestalt) of empty bladder which corresponds to the 'diastolic condition' of other authors is stated by Waldeyer to be less common in the male than in the female, and to be associated with the thinner bladder wall in the latter sex. As has been mentioned above, the 'diastolic form' of the organ very probably arises as the result of an escape of fluid by the urethra after the bladder wall has lost its power of contracting. If this view is correct, the more frequent occurrence of this form of bladder in the female probably depends on the shorter urethra and consequent easier escape of fluid in that sex. The thinner bladder wall found in these cases is quite consistent with the idea that this 'diastolic' condition is due to post-mortem changes. In the subjects which I have examined, the condition did not obtain in those in whom the various organs were most satisfactorily hardened.

<sup>1</sup> *Das Becken*, 1899, p. 451.

*The bladder at birth.*—The empty bladder in the new-born child does not exhibit the surfaces and angles just described for the adult organ, but when specially hardened before removal it is found to be torpedo-shaped (fig. 6). The long axis of the organ, which is directed downwards and backwards, lies between the bladder apex above and the internal urethral orifice below. The lateral border is not marked, but in the position where it will afterwards be found, there is distinct intersection of the bundles of muscle fibres composing the bladder wall. The urethral orifice lies not only on a lower level than, but also on a somewhat posterior plane to, the points where the ureters reach the bladder. Thus the part of the wall of the organ which will afterwards become converted into the base of the bladder looks, in the foetus, upwards and backwards. Corresponding to this position of the ureter opening and the basal surface of the bladder, the long axis of the seminal vesicle is directed downwards and backwards, instead of downwards and forwards, as it is in the adult. The lateral angles of the bladder are not present. If we look upon the foetal bladder as a tube, whose long axis is straight, and directed downwards and backwards from the bladder apex to the internal urethral orifice, the descent of the organ into the pelvis must be accompanied by a bending forwards of its lower end, in such a manner as to bring the urethral opening on to a plane anterior to the openings of the ureters—as it is placed in the adult. Such a bending of its axis may be a predisposing cause to the formation of the lateral angles of the bladder, since a tube when bent in such a manner upon itself tends to bulge laterally.

*Relations of the empty bladder.*—The superior surface of the bladder, looking into the pelvic cavity, is related to coils of the small intestine and of the pelvic colon. In the female it is also intimately related to the anterior surface of the uterus. Each of the infero-lateral areas described above is in contact with the fascia covering the pelvic surface of the obturator internus and levator ani muscles. Anteriorly, near the middle line, each of these areas rests against the pubic bone and symphysis and against the retro-pubic fat. The basal surface of the bladder is directed against the terminal portions of the

vasa deferentia and against the seminal vesicles. These structures separate the base of the bladder from the rectum. The vasa deferentia and the lower parts of seminal vesicles are very closely related to the bladder wall; the upper ends of the seminal vesicles, on the other hand, do not lie so close to the bladder, as they are directed somewhat backwards.<sup>1</sup> In the interval between the upper end of the seminal vesicle and the bladder wall, numerous veins are to be found which establish connections with the prostatic plexus. In this situation, also, a considerable amount of smooth muscular tissue is often present. Owing to the bending backwards of the upper end of the seminal vesicle, an interval is present between the summit of the vesicle and the lateral angle of the bladder (see fig. 4). Each seminal vesicle along its inner aspect is in contact with the vas deferens, and the vasa deferentia of opposite sides are in contact with one another in the middle line. In this way no interval is left below the peritoneal cavity in which the anterior wall of the rectum is in direct contact with the base of the bladder, at least when the latter viscus is empty (see fig. 8). It is not easy to explain how the area arises over which the bladder and rectum are in contact, when the former organ is distended, unless, indeed, distension of the bladder is accompanied by a relative raising of the level of the peritoneal reflection from the posterior part of the bladder on to the anterior surface of the rectum, or by a separation of the ampullæ of the vasa deferentia. No evidence that such a separation of the vasa deferentia takes place is to be found by a study of the specimens at my disposal; indeed, in the case of a somewhat distended bladder, the ampullæ of the vasa deferentia are found to be closely applied to one another in the middle line. In this specimen, however, the peritoneal reflection forming the bottom of the recto-vesical pouch appears to be somewhat raised, leaving a small area over which bladder and rectum are in contact. These facts lead me to believe that in the case of the moderately distended bladder, the area over which the bladder and rectum are in close relation is formed by a raising of the level of the peritoneal reflection, which forms the recto-vesical pouch. The obliterated hypo-

<sup>1</sup> This bending backwards of the upper end of the seminal vesicle, away from the bladder, was first pointed out to me by Prof. Birmingham.

gastric artery is not closely related to the empty bladder of the adult, but lies on the side wall of the pelvis from one to two inches above the level of the lateral border of the organ.<sup>1</sup> In one case only did this obliterated vessel touch the empty bladder, and here the unusual condition was present on the right side only; on the left side the vessel lay above the level of the bladder on the side wall of the pelvis. The vas deferens also crosses the side wall of the pelvis above the level of the lateral border of the bladder, until a short distance behind the point where it crosses the ureter is reached. Here the vas deferens turns inwards and downwards, and becomes related to the base of the bladder (fig. 7). The lowest portion of the bladder is connected with the prostate—the separation between the two organs being a purely artificial one. Superficially, a groove separates the under aspect of the bladder from the prostate, and this groove, which is deep and well marked laterally, lodges numerous veins connected with the prostatic plexus (figs. 4 and 13).

*Peritoneal connections of the empty bladder.*—The peritoneum covers the superior surface of the bladder, and leaves it along each lateral border to reach the side wall of the pelvis. The line of reflection of the peritoneum from the bladder to the side wall of the pelvis is an almost horizontal one, and corresponds to the lateral false ligament of the organ. The level of the line of peritoneal reflection varies somewhat, according as the point from which it starts anteriorly, namely, the bladder apex, lies a short distance above the upper margin of the symphysis pubis or on a lower level, and behind the symphysis.

When the peritoneum is traced backwards over the superior surface of the bladder, one often notices that, when the posterior border of the organ is reached, the peritoneum dips down to a slight extent, and then rises again to cover the vasa deferentia. The little peritoneal depression thus formed is seen in figs. 3, 7, and 8, and also in one of Waldeyer's sections; it appears to represent, when present, the utero-vesical pouch of the female.

Traced still further backwards over the vasa deferentia, the

<sup>1</sup> Waldeyer notes that the obliterated hypogastric arteries are not closely related to the empty bladder in the adult.—*Das Becken*, p. 299.

peritoneum often forms in the middle line of the body a small but distinct fold (the two layers of which may be in contact with one another), before it passes to the lowest part of the peritoneal cavity to be reflected on to the rectum. This fold is seen in section in figs. 7 and 8, while its appearance in the undissected pelvis is seen in fig. 3, which is a drawing from a subject in which the fold was very well marked. The pouch which lies behind and below the level of this fold is often described as a portion of the recto-vesical pouch, but it would seem to be more accurately described as a pouch lying between the rectum behind and the vasa deferentia and seminal vesicles in front. It appears to represent accurately the recto-vaginal pouch of the female, which lies below the level of the 'torus uterinus,' or representation in the female of the fold just described. When one traces this fold outwards from the middle line, it is found to be continued into a crescentic peritoneal fold which reaches backwards towards the sacrum (see figs. 3 and 7). These latter crescentic folds are by some authorities called *posterior false ligaments* of the bladder (Symington,<sup>1</sup> Cleland and Mackay,<sup>2</sup> and other authors), while from others they received the name of *recto-vesical* folds. These terms seem hardly suitable, as the folds undoubtedly pass rather to the vasa deferentia and seminal vesicles than to the bladder. The crescentic folds almost certainly represent the utero-sacral ligaments in the female, and like these latter they often contain, in their basal or thicker portions, much smooth muscular tissue. The small mesially placed fold which connects the two lateral portions, and which is seen in mesial section of the pelvis, will, in this case, represent the ridge—torus uterinus—sometimes observed crossing the posterior aspect of the cervix uteri and connecting the utero-sacral ligaments of opposite sides (see figs. 3, 7, 8, and 9). This view of the 'recto-vesical' folds appears to be the one accepted by Waldeyer. In nearly all cases in which the pelvic viscera have been satisfactorily hardened, the arrangement described is easily made out.

The term 'atrium of the pouch of Douglas' has been applied to the part of the peritoneal cavity which in the female lies

<sup>1</sup> *Quain's Anatomy*, vol. iii. part iv., 1896, pp. 211 and 115.

<sup>2</sup> *Human Anatomy*, 1896, p. 768.

behind the distended bladder and above the level of the folds just mentioned, and it seems satisfactory to restrict the term 'pouch of Douglas' to the part of the peritoneal cavity which lies below the level of the folds in question.<sup>1</sup> Should it be inadmissible to apply the terms 'folds of Douglas' (*plicæ Douglasi*)<sup>2</sup> and 'pouch of Douglas' (*cavum Douglasi*) to these structures in both sexes, one might venture to suggest that the term 'sacro-genital folds' and 'recto-genital pouch' would be applicable to these structures which are morphologically equivalent in the two sexes.

Figs. 8, 9, and 10 are diagrammatic representations of the arrangement of the peritoneum as seen in mesial section of the bladder. In fig. 10 alone does the peritoneum cover a portion of the basal surface of the organ, in the others it is borne off by the seminal vesicles and vasa deferentia. I am inclined, however, to look upon fig. 10 as representing a somewhat abnormal condition due to an escape of fluid from the bladder after death, as the organ possesses a concave upper surface, and is not very satisfactorily hardened. If this is so, the fold marked I in this figure very probably is an artificial production, and does not represent the folds marked similarly in other figures. If we exclude this unsatisfactory case, none of the specimens examined show the peritoneum to be directly related to any part of the basal surface of the empty bladder. In each of the others the peritoneal covering is confined to the upper surface.

In many specimens the peritoneum covering the superior surface of the empty bladder presents a transversely disposed fold or wrinkle. This fold—the *plica vesicalis transversa*—appears to have been first noticed by Henle,<sup>3</sup> and it has since received attention from Waldeyer<sup>4</sup> and others. Waldeyer makes use of the lateral continuation of the fold to subdivide the peritoneal fossa on each side of the bladder (*fossa paravesicalis*) into anterior and posterior portions. He appears to

<sup>1</sup> See, for instance, Waldeyer, *Das Becken*, p. 446.

<sup>2</sup> 'Plica recto-uterina' [Douglasi] occurs in *Die Anatomische Nomenclatur*, His, 1895, p. 66. See also Henle, *Lehrbuch der Anatomie des Menschen*, 1875, Bd. ii. p. 911.

<sup>3</sup> "Handbuch der systematischen Anatomie des Menschen," 1875, *Zweite Auflage*, Bd. ii. p. 910, and fig. 681.

<sup>4</sup> "Topographical Sketch of the Lateral Wall of the Pelvic Cavity," *Journal of Anatomy and Physiology*, Oct. 1897, *Das Becken*, 1898, and elsewhere.

consider that this fold prevents undue stretching of the peritoneum when the bladder becomes distended, and speaks of it as a reserve fold of the peritoneum (*Reservefalte*). I have found the fold to be very variable and to be often absent; it is seen to be well developed in the subjects from which figs. 3 and 7 were made. Sometimes more than a single transverse fold is present. When strongly marked the lateral continuation of the fold can be traced on to the side wall of the pelvis and over the pelvic brim towards the region of the internal abdominal ring. Observations made on the pelvis of the foetus lead me to believe that this *plica transversa* is not merely a '*Reservefalte*,' but that, in many cases at all events, it owes its origin to the same processes which in the foetus give rise to the inguinal pouches of the peritoneum. Fig. 11 is a drawing of the pelvis and lower part of the anterior abdominal wall of a foetus, in whom the testes have entered the inguinal pouches, but the latter still widely communicate with the abdomen by the internal abdominal openings. Stretching between the abdominal rings of opposite sides are to be seen a number of minute folds of peritoneum which lie parallel to one another in their course. These folds cross the obliterated hypogastric arteries and bladder. In some specimens a single fold is present in this position in the foetus, while more rarely all trace of such a fold is absent. One cannot help feeling that these folds found in the foetus almost certainly represent the *plica transversa* of the adult, which, in many cases, has an almost similar course, from one abdominal ring to the other across the hypogastric arteries and bladder. The descent of the bladder during development would account for the turning downwards of the fold into the pelvis in the adult. I have found this fold of peritoneum more frequently and better marked in the male than in the female foetus, and in one specimen of a full time male foetus the bladder was found to be distended, yet the fold was not obliterated. The portion of the fold which is nearest to the abdominal ring usually lies close to, and parallel with, the abdominal part of the vas deferens; the portion which crosses the bladder, on the other hand, often has the appearance of a transverse fold connecting the vasa deferentia of opposite sides. I believe that we are justified in



considering the drag on the peritoneal membrane accompanying the formation of the inguinal pouches to be the cause of the fold in the foetus; the fold appearing as a result of the stretching of the portion of the peritoneal membrane which lies between the abdominal rings. A further result of this stretching may be found in the obliteration of the lower portions of the deep peritoneal recesses which exist between the obliterated hypogastric arteries and the anterior abdominal wall. It is interesting in this connection to notice, that the adult specimen in which the fold was found most extensively developed was one in whom there existed a slight inguinal hernia which contained a portion of the vermiform appendix. This specimen is represented in fig. 7. Considered along with this case the figure given of the fold by Henle<sup>1</sup> is of extreme interest, as the specimen shown by him illustrates the fold passing from the region of the sac of a right inguinal hernia to that of a left femoral hernia. In this case a change in the direction of the drag on the peritoneum seems to have caused a corresponding change in the direction of the fold.<sup>2</sup>

In specimens still younger than that represented in fig. 11, at a period when the testes have reached but not entered the inguinal pouches, a very distinct fold of the peritoneum is to be seen stretching across between the testes, which in its course crosses the bladder and hypogastric arteries (see fig. 12). This latter fold has been figured by Henle,<sup>3</sup> and by him it is considered to represent the future plica recto-vesicalis.

Waldeyer refers to Henle's figure, and accepts his interpretation. It does not seem possible that this fold, which in the foetus is found to pass across from the region of one inguinal canal to the other, could represent the folds which, later on, are found to be directed backwards towards the sacrum. In fact, a study of numerous specimens affords no evidence that this peritoneal fold is gradually transformed into the recto-vesical ligaments, but it appears more probable that it owes its origin to a stretching of the portion of the peritoneal membrane which

<sup>1</sup> *Loc. cit.*, p. 909, fig. 681.

<sup>2</sup> Since this paper was written I have seen the fold of peritoneum stretched across between the crural canals of opposite sides in a subject with double femoral hernia.

<sup>3</sup> *Loc. cit.*, p. 911, fig. 682.



lies between the testes as the latter pass towards the inguinal canals. Its origin is probably due to the similar causes which at a later period give rise to the plica transversa. Indeed it is possible that the fold in question may be transformed into the plica transversa (compare figs. 11 and 12).

The actual attachments of the peritoneal fold are difficult to determine, but it appears to be connected more directly with the gubernaculum than with the testis. If we are to look upon the fold shown in Henle's figure and in fig. 12 of this paper as the source of the plica transversa, then this latter arises at an earlier period in the male than in the female foetus. Henle considers that the fold shown in his figure is representative of the fold which in the female forms the broad ligament, and states that it is connected with the mesorchium as long as the testes remain immediately below the kidneys.

#### THE SHAPE OF THE PROSTATE.

In the male subjects examined the prostate, inclosed within its fibrous capsule, was found to be very constant in shape. Superficially, the prostate is separated by a deep groove from the bladder, and this groove is especially well marked laterally. The groove when viewed from the side is seen to be directed downwards and forwards, but when seen from behind its direction is almost horizontal. As the separation between the bladder and the prostate is a purely artificial one, and must be affected by the use of a knife, we may consider, for convenience, the plane determined by this groove as separating bladder and prostate. It is quite true that some of the glandular tissue usually ascribed to the prostate may lie above this plane, and that the muscular wall of the bladder may often be traced into the tissue below it. If a knife be used to sever the bladder from the prostate in the plane just indicated, we find that the prostate so separated is a somewhat conical body, whose base, directed upwards and forwards when in position, corresponds for the most part by the plane of the section. A small portion on each of the base is, however, free, and forms the lower border of the deep sulcus between the bladder and the prostate. In outline the base is triangular, one of the angles

being placed anteriorly, the others laterally. The apex of the prostate is rounded and points downwards, and from it a rounded border is directed to each of the angles of the base. The three borders so determined separate three surfaces—namely, a posterior, and a right and left lateral surface. The posterior surface is flat, and looks downwards and backwards towards the rectum, while each lateral surface is convex from above downwards and forwards. The lateral surface looks outwards and a little downwards and forwards for the most part; its upper and posterior part, however, looks directly outwards, or outwards and backwards (see fig. 13). The orifice of the urethra does not pierce the apex of the prostate, but is placed on the border, separating the lateral surfaces at a point a short distance above and in front of the apex (figs. 9, 10, and 13). This position of the urethral opening relative to the apex of the prostate is observed also in the child at birth (fig. 6).

#### EXPLANATION OF PLATES XXVIII.-XXX.

[Reference letters common to all figures except No. 12]

- |  |                                    |
|--|------------------------------------|
| A. Deep epigastric artery.             | J. Cavum Douglassi (Recto-vaginal) |
| B.b. Bladder.                          | or 'Recto-vesical' pouch.          |
| C. Colon or rectum.                    | L. Common iliac artery.            |
| D.d. Hypogastric artery.               | N. Psoas muscle.                   |
| E.e. Plica vesicalis transversa.       | O. External iliac artery.          |
| F. Vas deferens.                       | P.p. Prostate.                     |
| H.h. Ureter.                           | r. Vermiform appendix.             |
| I.i. Plica Douglassi (Utero-sacral) or | U. Urethra.                        |
| 'Recto-vesical' fold.                  | W. Pubic bone.                     |
|  | X. Seminal vesicle.                |

Fig. 3. View of the pelvis of a young male subject, seen from above and behind. The peritoneum has been left *in situ*, and the various structures are seen shining through it.

Fig. 4. Cast of the empty bladder and the prostate, seen from the side. The peritoneum has been left upon the superior surface of the organ, and its cut edge—indicated by a white line—corresponds in position to the lateral border of the bladder. The point where the urethra leaves the prostate lies close to the letter U in the figure.

Fig. 5. Cast of one-half of the bladder and prostate, seen from below (same specimen as fig. 4). The point where the urethra leaves the prostate is indicated by a black dot near P in the figure.

Professor DIXON on the Form of the Empty Bladder.

FIG. 3.

FIG. 5.

;

FIG. 4.

FIG. 6.



,

FIG. 7.

FIGS. 9 and 10.

FIG. 8.

FIG. 13.



FIG. 11.

FIG. 12.





Fig. 6. Bladder and prostate of a new-born child, seen from the side. The bladder is spindle- or torpedo-shaped. Note the forward position of the junction of the ureter with the bladder, and the direction of the seminal vesicle. Some muscular fibres connected with the bladder are seen in front of the prostate and urethra. These, when the organ was in position, were attached to the pubis.

Fig. 7. Mesial section of the male pelvis. The portions of intestine which lay in the pelvis have been lifted out to show the side wall of the pelvic cavity. The peritoneal folds of the pelvis and the various structures which appear shining through the peritoneum lining the cavity, can be made out.

Fig. 8. Mesial section through the bladder (same specimen as figs. 4 and 5). The cut edge of the peritoneum is shown by a white line. Owing to an interlocking of the curves described by the vasa deferentia, both right and left vessels (F) are cut in this section.

Figs. 9 and 10. Mesial sections of the bladder from two different subjects to illustrate differences in the arrangement of the peritoneum in relation to the organ. In both cases the cut edge of the peritoneum is indicated by a white line. The condition in fig. 10 is probably due to a post-mortem change in the bladder. (See text.)

Fig. 11. Pelvis and posterior aspect of the anterior abdominal wall in a male foetus of the eighth month. The internal abdominal rings and plica vesicalis transversa are well seen.

Fig. 12. View of a portion of the posterior aspect of the anterior abdominal wall of a younger foetus than that shown in fig. 11. The testes have not descended, but are seen lying to the outer sides of the hypogastric arteries. They are connected by a peritoneal fold which stretches across the hypogastric arteries and bladder. The gubernaculum is seen on the left side, but not lettered. B. bladder, D. hypogastric artery, P. epididymis, S. peritoneal fold, T. testis.

Fig. 13. Prostate and somewhat distended bladder, seen from the side. The shape of the prostate and the deep groove between the prostate and bladder are well seen. The dotted line indicates the level at which the peritoneum was reflected from the bladder. The relationship of the apex of the prostate to the point of exit of the urethra is clearly indicated.

ON THE STRUCTURE AND FUNCTIONS OF HÆMO-  
LYMPH GLANDS. By W. B. DRUMMOND, M.B., C.M.,  
M.R.C.P.E.<sup>1</sup> (PLATES XXXI.-XXXIII.)

THE structures variously termed hæmal glands and hæmolymph glands have long been known, but only in quite recent years has any adequate description been given of their minute anatomy, and quite divergent views have been brought forward as to their probable function. Our knowledge of their distribution among the mammalia is still very imperfect. They are so easily overlooked in some cases, and so easily mistaken for other structures, that it is probable they may be present in many species where they have not yet been discovered.

1. BIBLIOGRAPHICAL.

The structures now generally known as hæmolymph glands were first described by Heneage Gibbs in a paper in the *Quart. Journ. of Micr. Sci.*, vol. xxiv. (1884), "On some Structures found in the Connective Tissue between the Renal Artery and Vein in the Human Subject."

W. F. Robertson afterwards described them more fully in the *Lancet* for 29th November 1890.

In 1891 Clarkson published in the *Brit. Med. Journal* a "Report on Hæmal Glands," describing certain glands which he found in close relationship with the renal artery in certain herbivora, viz., the horse, sheep, and pig.

In a *Text-book of Histology*, 1896, Clarkson describes two varieties of hæmal gland, viz., those previously described by himself, and those described by Robertson as hæmolymph glands.

In the *Journal of Anat. and Phys.* (January 1897), Swale Vincent and Spencer Harrison published an excellent description of the "Hæmolymph Glands of some Vertebrates." They

<sup>1</sup> The work for this paper was carried out in the laboratory of the Royal College of Physicians in Edinburgh.

give a much more detailed description of the glands than previous writers, and come to quite different conclusions as to their function. Robertson and Clarkson, though for different reasons, believe that the glands are concerned in the formation of red blood corpuscles, while Vincent and Harrison believe that they are concerned not in blood formation but in blood destruction.

In the present paper some points in the minute structure of the glands are described in detail, and the different views brought forward as to their function are discussed. For the purpose of the paper the hæmolymp glands of the sheep and ox, of the rat, and of the dog are examined, as these present well marked varieties in structure. Some notes are also given on the development of the glands.

## 2. METHODS.

Most of the specimens were fixed in a saturated solution of corrosive sublimate in normal salt solution, and afterwards thoroughly washed in running water or in normal salt solution, or in dilute alcohol and iodine. Formaline, osmic acid, Cox's fluid, and other fixatives were also used.

All the specimens were cut in paraffin. The sections were fixed to the slide by the hot-water method, and stained on the slide.

The stains chiefly used were Ehrlich's hæmatoxylin and eosin or acid fuchsin or aurantia; methylene blue and eosin; the Ehrlich-Biondi triple stain; hæmatoxylin, saffranin, and eosin; Haidenhain's hæmatoxylin and iron-alum; Cox's modification of Golgi's method.

Fresh specimens and cover-glass preparations were also examined.

## 3. GROSS ANATOMY.

(a.) *Bos Taurus and Ovis Aries*.—The gross anatomy of the hæmolymp glands of the sheep and ox need only be described briefly. For further particulars the reader is referred to the descriptions already published by Robertson and by Vincent and Harrison.

In the sheep, the hæmolymp glands are very conspicuous

objects, appearing like little clots of blood amongst the surrounding fat. They are found chiefly in the subvertebral region, and are most numerous in the abdomen, but are by no means scarce in the thoracic and cervical regions. In the cervical region they have been mistaken for parathyroid glands. In the thorax they are found chiefly in the posterior and in the middle mediastinum, and in the connective tissue at the root of the lungs. In the abdomen and pelvis they abound in the prevertebral fat, and may extend for some distance into the mesentery, but not so far as the bowel. They appear to be absent from the appendices epiploicæ. They always have tolerably large vessels passing to them.

The size of the glands varies considerably. In the sheep they are rarely larger than a small pea; in the ox they are frequently about as large as a broad bean. They are usually oval in form, and their greatest diameter varies from about 2 mm. to about 2 cm. Their number has been estimated by Robertson to be between three hundred and four hundred in the sheep. They are not difficult to find. On the contrary, their red colour, and their position, embedded in the white fat of the subvertebral region, render them very conspicuous, and one is not surprised to find that they are well known to butchers and meat inspectors, although they have attracted so little attention from histologists. The smaller glands might readily be mistaken for drops of blood amongst the fat, a mistake which might be apparently confirmed if too rough an attempt were made to remove a gland, as the thin capsule readily ruptures, allowing a drop of blood to escape. Some of the smaller glands, indeed, have the appearance of being simply thin-walled sacs containing a drop of blood. The larger glands, on the other hand, might be taken for congested lymphatic glands, but it can readily be made out that they contain a much larger amount of blood than congested lymphatic glands would do, and that this drops from them when they are cut across. Indeed, in a large gland it can be made out by the naked-eye examination alone that under the capsule of the gland there is a sinus filled with blood, and that other similar sinuses are present in the interior of the gland. The gland has, like a lymphatic gland, a hilus into which vessels enter.

It has not yet been determined when hæmolymp glands appear in the foetus, but in a foetal calf measuring 9 inches in length there were found in the connective tissue in front of the spine a number of minute red dots which, on microscopic examination, proved to be unmistakable hæmolymp glands. These are described in a later section.

(b.) *Canis familiaris*.—Vincent and Harrison failed to find any typical hæmolymp glands in the dog, but describe lobulated structures, partly red and partly pale yellow in colour, which in section resembled lymphatic glands in structure, except that here and there the peripheral sinus contained red blood corpuscles, in some cases abundantly. This distinction is obviously an important one. We have had little difficulty in finding in most of the specimens of the dog examined, in addition to such glands as the above, others which contained not only a peripheral, but large central blood-containing sinuses. These glands often closely resembled lymphatic glands to the naked eye, indeed, in many instances were almost indistinguishable from them, but differed from them greatly in their minute structure; and although they differed also from the hæmolymp glands of the sheep, they may quite as well be considered 'typical' as the latter. Being so easily mistaken for ordinary lymphatic glands, they require to be carefully searched for. They can often be distinguished by the presence of irregular patches of rosy or red colour on the surface. They are to be found in the prevertebral fat of the abdomen and pelvis, and in the neighbourhood of the renal artery. They can frequently be found at the brim of the pelvis in the fat just behind the common iliac artery, and in some instances a chain of similar glands can be found in the fat behind the aorta, extending up to the level of the renal artery. The glands at the pelvic brim are sometimes rather large. In an old retriever they measured 1.25 cm. in their longest diameter. No hæmolymp glands were found outside the abdomen.

In a very fat pug dog examined, a few minute rusty spots were found in the prevertebral fat when cut across. These looked just as if a minute vessel had been divided and a little blood had oozed on to the cut surface. On microscopic examination, these were found to be minute hæmolymp glands with very thin capsules, and containing a large amount of pigment. The

ordinary hæmolymp glands were not found in this specimen, possibly owing to the great amount of fat, which rendered the search difficult. Hæmolymp glands obtained from young puppies had a closer resemblance to those found in the sheep than had any of those obtained from older animals.

(c.) *Mus rattus*.—In the rat hæmolymp glands can almost always be found in the form of one or more, often two, small oval or lenticular bodies at the lower border of the pancreas, to the left of the middle line. These are usually in apposition. They are oval in outline, flattened from before backwards, and measure from 2 to 3 mm. in their longest diameter. They are of a rusty colour, and sometimes appear paler in the centre than at the periphery.

Slightly to the left of these, and close to the left kidney, there can usually be found one or two other glands, paler in colour, more spherical in form, and slightly irregular on the surface, having in fact a mulberry-like appearance. These two varieties of gland can be found with great constancy in the situations described, but one or other may be absent. As a rule, no hæmolymp glands were found elsewhere. Indeed, the above description was found to hold true for nine out of ten rats examined consecutively. In the tenth no hæmolymp glands were discovered at all. Vincent and Harrison describe the occurrence of three or four small glands "in the fat, in relation to the gastro-splenic omentum."

#### 4. HISTOLOGY.

The hæmolymp glands of the sheep and ox, of the dog, and of the rat differ markedly from one another in their minute structure, yet these differences mainly result from the variable prominence of certain structural features present in all. It is therefore possible and convenient to give in the first place a general description of the minute structure of hæmolymp glands.

The simplest and smallest hæmolymp glands found in the adult consist simply of a minute rounded or oval mass of lymphoid tissue, surrounded by a thin capsule of connective tissue, but separated from it by a narrow space or sinus in which a few red blood corpuscles can be seen.

In glands slightly larger than the above, the lymphoid tissue is found not to be perfectly uniform in structure. Immediately under the peripheral sinus the lymphoid tissue forms a very compact zone, the cells of which are densely crowded together and stain deeply. In the case of the sheep and of the dog a circle of germ-centres may be present in this zone, and in large glands from the ox a double circle of germ centres may be present. When the germ-centres reach some size, the cells at their periphery stain very deeply, so as to form a dark-coloured ring round the centre, the cells of which stain very slightly, and in some specimens hardly at all. Numerous mitotic figures can usually be seen in the germ-centres. The lymphoid tissue in the centre of the gland is less compact and stains less deeply than the peripheral portion. It is often arranged in masses or strands between which are spaces lined by thin endothelial layer, and containing, like the peripheral sinus, no blood corpuscles. The peripheral sinus, also, is lined by an endothelial layer which covers the lymphoid mass, and is reflected over the trabeculæ, which in large specimens pass from the capsule into the interior of the gland.

The proportional area occupied by the blood sinuses varies greatly. In some specimens the lymphoid tissue is nearly as abundant as in an ordinary lymphatic gland. In others, and especially in specimens from the sheep and ox, the gland may consist practically of an aggregation of blood sinuses, with here and there a small islet of lymphoid tissue.

### THE CONNECTIVE TISSUE.

The capsule of the gland is composed of white fibrous tissue, and yellow elastic fibres and non-striped muscle may also be present. It varies very greatly in thickness. In lambs it is often remarkably thin. In the ox it may be very thick, the fibres being loosely arranged, and containing between them irregular spaces which are filled with blood. Near the peripheral sinus these spaces become larger, and the connective tissue less abundant, so that no sharp line of demarcation can be drawn between the capsule and the sinus.

From the capsule trabeculae of fibrous tissue may pass into the interior of the gland. In some cases these trabeculae are of large size, and the arrangement of fibrous tissue is practically the same as in an ordinary lymphatic gland. In some instances, even in large glands, no definite trabeculae are present. In all instances, however, an adenoid reticulum of fine fibres crosses the peripheral sinus, and throughout the lymphoid tissue a close network of fine connective tissue fibres is present. In some specimens stained by Cox's modification of Golgi's method, the blackening affected the connective tissue fibres, which were found to form a remarkably close feltwork both in the sinuses and throughout the lymphoid tissue. In sections stained in this way, the amount of connective tissue was seen to be very much greater than would be imagined from an examination of specimens stained by any of the ordinary methods. The thicker trabecular strands give off finer lateral strands, which divide and subdivide so as to form ultimately a network of exceedingly fine fibrils, the meshes of which, as seen in section, are scarcely larger than the individual lymphocytes of the lymphoid tissue. Where the network is present in the blood sinus, it must greatly retard the circulation through it. The central sinuses are often comparatively free from connective tissue strands.

#### THE LYMPHOID TISSUE.

The lymphoid tissue varies very greatly in amount and in arrangement, even in the same species of animal. In some cases the gland may be composed almost entirely of a mass of lymphoid tissue. In other cases the section may have the appearance of a lake of blood, containing one or two small islands of lymphoid tissue, which may be moored to the capsule by fine strands of connective tissue.

In some specimens the structure and general arrangement of the lymphoid tissue closely resembles that of lymphatic glands. Some such glands found in the neighbourhood of the renal artery have been described by Clarkson as a special variety, and were named by him hæmal glands. There does not seem to be any sufficient reason for placing these in a group by them-



selves. The division of the lymphoid tissue into a cortical and a medullary portion, and the occurrence of germ-centres, has already been mentioned. In the dog, germ-centres are less abundant than in the sheep and ox. In the rat no distinct germ-centres were seen, but the cortical portion of the lymphoid tissue often has a crenated outline (which gives the gland a lobulated or 'mulberry' appearance to the naked eye), with a peripheral zone of lymphocytes closely crowded together.

Between the germ-centres and in the medullary portions of the gland the leucocytes are less crowded together, and their nuclei stain less deeply than do those of the germ-centres, or, at any rate, of their peripheral zones. In the medulla the lymphoid tissue is usually arranged in strands or columns of greater or lesser thickness, between which are the central blood sinuses of the organ.

#### THE VARIETIES OF CELLS.

A considerable variety of cells enters into the formation of the glands. These have been described by previous writers according to the appearances presented, but as most of the cells belong to the leucocyte class, it will simplify the description and add to its clearness to make use of the terms now usually applied to the ordinary classes of leucocytes. It would be out of place in the present paper to offer any discussion as to the relation of the different varieties of leucocytes to one another. Whether leucocytes can be divided into fixed and definite varieties, or even into hæmic and coelomic groups, as Kanthack and Hardy have tried to do, or whether, as Everard, Gulland, Ruffer, and others maintain, all varieties are to be regarded as modifications of one another (except, perhaps, in their most specialised forms), may be left an open question. For our present purpose the lymphocyte may be considered as representing the primitive cell from which all varieties of leucocytes may be derived, and the large hyaline leucocyte, the eosinophile, and the coarsely-granular basophile as representing the terminal results of these streams of development, the cells of which cease to be interchangeable at some at present undetermined point.

(a.) *Lymphocytes*.—These are by far the most numerous cells in the lymphoid tissue. They are small cells, spherical or nearly spherical in form. Their protoplasm is scanty, forming as a rule a very thin layer surrounding the nucleus. The nucleus is round or somewhat oval in outline, and contains a chromatin network, in which the chromatin is aggregated into nodules, so as to give the nucleus a granular appearance. In many cases one, two, or even three of these nodules may be of comparatively large size, in which case they have the appearance of nucleoli, especially as the network cannot always be distinctly made out. These cells are extremely numerous, especially at the periphery of the germ-centres, where, on account of the deepness with which their nuclei stain, they may form a dark ring, in striking contrast to the pale central portion whose cells may stain very lightly. In other cases all the cells stain deeply. Perhaps the most striking feature of these collections of lymphocytes is the very close resemblance of the cells to one another in size, form, and appearance. But one has only to pass slightly away from one of the germ-centres and examine one of the thinner strands of lymphoid tissue, usually close at hand, to find a greater variety in the appearance of the cells. Typical lymphocytes are present in abundance, but among them are numerous cells which differ from them only in the fact that their protoplasm is more abundant. In others, again, the nucleus is also larger, so that the cell looks like a very large lymphocyte. These cells also vary more in shape. In the adjacent sinus these cells and lymphocytes are also present, and all gradations may be found between them and hyaline leucocytes.

(b.) *The Hyaline Cells*.—Hyaline cells may be present in great abundance in the sinuses, especially in the glands of the dog and the rat. They are larger, usually very much larger, than the lymphocytes, and are especially characterised by the large size of the cell-body, whose diameter may be six or eight times as great as that of the lymphocyte. Although some authorities regard it as very probable that some hyaline cells, at any rate, are derived not from lymphocytes, but from the epithelial cells lining the lymph and blood channels, there is nothing in the appearances seen in the hæmolymph glands to support this view. All transitions can readily be discovered between the

hyaline cells and the lymphocytes, and the latter may be regarded as the sole source of the former.

The nucleus of the hyaline cell is usually round or oval; it may be slightly curved, or even horseshoe-shaped. Its structure is the same as that of the lymphocyte, but the meshes of the chromatin network are wider, and the network more distinct. The body of the cell is composed of clear protoplasm, and as the cells are amoeboid and phagocytic, their form naturally varies greatly.

Inclusions of various kinds are commonly found in the protoplasm. The most common of these are red blood corpuscles. These can be recognised by their shape and size, and by the fact that their staining reactions are exactly like those of red corpuscles which are free in the sinus. Many of the hyaline cells contain several red corpuscles in their interior, and here and there can be found a large cell which contains twenty or thirty of the red cells, and looks like a small sac filled with blood.

Fragments of nuclei in various stages of degeneration are not uncommon in the protoplasm of the hyaline cells. Pigment is frequently present, sometimes in the form of minute granules, at others of larger masses, which with transmitted light have a golden yellow colour. In sections treated with dilute hydrochloric acid and a solution of ferrocyanide of potassium, the pigment changes to a blue colour.

Occasionally hyaline cells can be seen undergoing division by mitosis. These phagocytic cells vary greatly in abundance in different glands and in different species of animal. In the sheep and ox, for example, the sinuses are invariably filled with blood, and it is only here and there that one can discover a hyaline cell with red corpuscles or pigment in its interior. Such cells, however, do occur, and are much more numerous in some specimens than others. In the rat the sinuses may be filled with red blood corpuscles, but in some glands hyaline cells are very abundant, and may even be the most conspicuous cells in the section. Some of the sinuses may be crowded with them, and in some cases nearly all the red corpuscles visible are in the interior of these cells.

This condition of things may exist to a still more marked

degree in the hæmolymp glands of the dog. Here the sinuses may be completely blocked by a mass of large hyaline cells, which are so closely packed together as to present the appearance of a solid tissue. Most of these cells may contain a number of red cells in their interior, while no red cells are present between them. The sinuses are evidently blocked by the mass of hyaline cells. These appearances are described more fully in a later section.

(c.) *Acidophile Cells*.—Under this term may be included the neutrophile and amphophile cells of Ehrlich (finely granular oxyphile), and the eosinophile (coarsely granular oxyphile).

It is unnecessary to describe the appearances presented by these cells in detail. The finely granular oxyphile cells are relatively to other forms of leucocytes less abundant than they are in the blood of the general circulation. Their numbers vary greatly in different specimens. In specimens from young animals they may be abundant, and are sometimes found in little groups in the corner of a sinus, or even in lymphoid tissue, the cells of which are only loosely aggregated. They are small cells, with lobate nuclei, subdivided into two, three, or more, and finely granular protoplasm. They are actively amoeboid, and this is indicated in sections by the great irregularity of their form.

Eosinophile cells are not uncommon, and in some specimens are even abundant. They are most frequent in the sinuses, but may also be seen in the interspaces between the connective tissue fibres of the capsule. I have not noticed any undergoing mitosis.

(d.) *Basophile Cells*.—Basophile cells are sometimes seen. They are rather large cells, measuring three or four times the diameter of the lymphocytes, and in sections stained with methylene blue and eosin they may be rather conspicuous. They occur principally in the sinuses, and also in the interstices of the connective tissue.

Compared to the other varieties of cells, their number is small. A section through the centre of a hæmolymp gland from the rat showed about thirty of them in the peripheral sinus. Others were present in the central sinuses. Other varieties of cell present were much too numerous to count.

(e.) *Giant Cells*.—Giant cells exactly like those which occur

in bone marrow may be present in hæmolymp glands. They are, however, extremely rare. I have found them in the calf, in the rat, and in the dog (puppy), but have not seen more than half a dozen altogether in many hundreds of sections.

### THE CIRCULATION.

Most information as regards the circulation through the gland has been gained by the examination of serial sections through entire glands. Two dogs were carefully injected, but after injection it was impossible to distinguish the hæmolymp glands from lymphatic glands, and no good specimens were obtained. Nevertheless, in the normal gland the blood filling the blood channels forms a natural injection whereby the main features of the circulation can be traced. The course of the circulation varies considerably in detail in different specimens; consequently only a very general description can be given. The following is a description of the course of the circulation through a sheep's gland:—

A fairly large artery passes to the hilus of the gland and, as it enters, divides into several branches. These pass into the gland along with the connective tissue, which also passes in at the hilus, and very rapidly subdivides into smaller and smaller branches, so that, a short distance from the hilus, only very minute vessels can be seen. These are still in the connective tissue of the gland. Ultimately these vessels end in dilated capillary spaces, which communicate with the general sinus system of the gland. All the sinuses communicate freely together. Ultimately the blood is collected in two or more very thin-walled venous channels, which unite in the centre of the gland to form a larger vein, which passes out at the hilus. The circulation through the gland must be extremely slow, for not only is the area occupied by the sinuses enormously larger in all dimensions than the sectional area of the arteries entering the gland, but the sinuses are themselves, for the most part, traversed by an extremely close feltwork of fine connective tissue fibres. Some of the central sinuses, however, may contain very little connective tissue. The germ-centres

are traversed only by small capillary spaces, which can only be made out in sections when they contain blood. The blood entering the gland seems, therefore, for the most part, to be conveyed rapidly to the peripheral portions of the gland, from which it percolates slowly through the system of sinuses to the centre of the gland, there to be collected by venous channels arising directly from the sinuses.

In the rat the arrangement of the arteries is somewhat different. The arteries penetrate more deeply into the gland, and many of them leave the connective tissue and pass into the lymphoid tissue, so that one often finds a section of an artery in the centre of a rounded mass of lymphoid tissue, reminding one of the appearance seen in the splenic corpuscles.

In the dog the most noticeable feature of the circulation is the number and large size of the arteries which enter and pass to all parts of the gland. The arteries may enter not only at the hilus, but through other parts of the capsule. In old dogs especially they have remarkably thick coats, so that they appear very conspicuous in sections; but even in the case of puppies only a few days old the number of distinct arteries passing deeply into the glands is a very noticeable feature. They are usually surrounded by a small amount of connective tissue, but may pass into the lymphoid tissue. In specimens obtained from puppies the sinuses were comparatively large, and in some cases were filled with blood, as is usual in the case of the sheep. In other specimens, hyaline cells were very abundant among the red cells. In others, again, the hyaline cells were so numerous that they had become closely packed, and were polygonal in outline, and completely filled many of the sinuses. Nevertheless, in most cases numerous minute capillary spaces, containing red corpuscles, were present between the hyaline cells, and bounded directly by them. A similar condition has already been described as occurring in the sinuses of older dogs; but in the case of the youngest puppies examined the above condition was present without there being any evidence of phagocytic action on the part of the hyaline cells. That is to say, the hyaline cells contained no inclusions, whether of red blood corpuscles or of pigment. In other parts of the same sections, however, hyaline cells containing red corpuscles were present.

## DEVELOPMENT.

No description has as yet been given of the development of hæmolymp glands. Vincent and Harrison express the opinion that they are probably developed from ordinary lymphatic glands. It is certainly the case that hæmolymp glands can be found which differ but little from lymphatic glands in structure. But while it is possible that, in some instances, they may be developed from them, there is no proof that this really occurs, and it seems more probable that they are separate structures from the first. This view is supported by the following considerations:—In the first place, their distribution does not in any respect correspond to that of lymphatic glands. There are numerous situations where lymphatic glands are invariably abundant where hæmolymp glands have never been discovered. Then, again, the hæmolymp glands have, as already described, a comparatively restricted distribution of their own, and although in species where these glands are very numerous this can only be described in general terms, in animals where they are present in small numbers, as in the case of the rat, it can be made out that their distribution is very constant. Lastly, at a comparatively early stage in the development of the lymphatic structures in the embryo, the hæmolymp glands are quite readily distinguishable from ordinary lymph glands, even to the naked eye. These considerations—although it may be admitted that they are not quite conclusive—seem all to point in the same direction, namely, to the conclusion that hæmolymp glands are structures *sui generis*, and not simply local modifications of lymphatic glands. Nevertheless, the earliest stages in the development of the hæmolymp glands may, and probably do, run parallel to those of the true lymphatic glands.

The lymphatic system arises in the embryo from spaces between the cells of the general parenchyma of the body. These give rise in time to a definite system of vessels. The lymphatic glands arise from lymphatic plexuses, which may be found characteristically at the flexures of the joints, and are recognisable before they contain any leucocytes. The first



leucocytes to appear in the blood of the embryo are of the wandering variety. These tend to leave the blood capillaries in the neighbourhood of the lymphatic plexuses, in the meshes of which they are caught. Here they greatly increase in numbers, partly by continued emigration from the blood-vessels, and partly by undergoing cell division. In this way the adenoid tissue of the gland is formed. Whatever be the early history of hæmolymp glands, beyond this stage they are quite distinct from lymphatic glands. In a foetal calf, which measured about nine inches from the nose to the root of the tail, a number of hæmolymp glands were discovered at different stages of development. Through the peritoneum covering the posterior abdominal wall, several minute red spots were seen, the largest of which measured from  $\cdot 5$  to  $\cdot 75$  mm. in diameter. Ordinary lymphatic glands, for the most part larger than the above, were quite common. Some of these little red bodies were found on microscopical examination to be quite well-formed hæmolymp glands. Each of them had a thin connective tissue capsule, a reticulum of fibrous tissue with leucocytes in the meshes, and numerous red corpuscles in capillaries and irregular spaces. In the smaller and simpler glands the leucocytes were not so numerous, that is, not so closely packed, as in ordinary lymphoid tissue, so that the fibrous stroma could be distinctly seen. Throughout the whole gland red corpuscles were very numerous, in some specimens much more numerous than the white cells, and were contained either in definite capillaries or in irregular spaces between the leucocytes. In some of the glands the red corpuscles formed a distinct layer just under the capsule, round whole or part of the circumference of the gland, thus giving rise to a rudimentary peripheral sinus, and in such cases it could sometimes be noticed that in the back of the gland furthest from the hilus, the leucocytes were becoming more densely packed, while the spaces containing red corpuscles were less abundant than in the simpler (earlier) stages just described, or than they still were in the centre and near the hilus of the gland.

In two puppies examined at the age of three days, hæmolymp glands were readily found at the brim of the pelvis. In some of these the sinuses occupied a relatively larger proportion of the



gland (roughly speaking, rather more than half of the sectional area) than is usual in adult dogs. In their structure these glands closely resembled those found in older dogs, the principal difference being that pigment was almost entirely absent, while in old dogs it is always exceedingly abundant. In these glands a number of hyaline leucocytes were present in the sinuses, and in some were so abundant as to fill some of the sinuses in the manner already described. Here and there a hyaline cell might be seen containing one or two red corpuscles in its interior. The vast majority of them, however, were quite free from inclusions of any kind. Hæmolymp glands from a puppy nine weeks old contained large numbers of hyaline cells with red corpuscles or pigment in their interior; in some glands the pigment was in rounded irregular masses, which were so abundant as in some parts of the gland to practically fill the sinuses, and to give their sections of the gland a rusty appearance to the naked eye.

#### CHARACTERISTIC FEATURES OF THE HÆMOLYMPH GLANDS OF DIFFERENT ANIMALS.

To illustrate the manner in which the hæmolymp glands of different species may characteristically differ from one another, the special features of the glands in the species here considered may be conveniently set down together.

##### *Sheep and Ox.*

*Lymphoid tissue* usually divided into cortical and medullary portions. Germ-centres usually abundant, in one or two rows.

*Sinuses* well developed, peripheral and central, often occupying the greater part of the area of the gland; filled with red blood corpuscles; leucocytes of the same varieties as in normal blood common in the sinuses; hyaline leucocytes containing red corpuscles or pigment often present, but usually very scanty.

*Pigment* moderate in amount or scanty.

*Arteries* entering gland rapidly break up into small vessels.

*Rat.*

*Lymphoid tissue* cortical and medullary. Cortical portion forms a dense peripheral zone, but distinct germ-centres are absent.

*Sinuses* large, peripheral and central, sometimes filled with red corpuscles, sometimes partially empty; hyaline cells common, sometimes very numerous, and usually containing red corpuscles or pigment.

*Pigment* usually moderate; sometimes abundant, especially in peripheral sinus.

*Arteries* pass deeply into the gland, and are often surrounded by lymphoid tissue.

*Dog.*

*Lymphoid tissue* cortical and medullary; germ-centres common in cortical zone. General arrangement may closely resemble that of a lymphatic gland.

*Sinuses* sometimes small, and may be peripheral only; usually fairly large, peripheral and central; may be filled with blood; more often partially or completely occupied by large hyaline cells, which as a rule contain many red blood corpuscles or pigment.

*Pigment*, except in the case of very young animals, extremely abundant, even to the extent of blocking some of the sinuses.

*Arteries* large and very numerous; penetrate to all parts of the gland; usually surrounded by connective tissue, but sometimes by lymphoid tissue.

## FUNCTION.

Hæmolymp glands are so numerous in some animals, and so constant, not only in their presence but in their general arrangement, in others, that they are obviously of considerable functional importance. Their structure would lead one to suppose that they perform some of the principal functions of lymphatic glands, and that they have in addition some function with reference to the red corpuscles. The constant presence of adenoid tissue more or less abundant, and the usual presence of germ-centres in which cell-division is actively going on, indicate

that the glands serve as active centres for the manufacture of leucocytes. It is an obvious suggestion that the arrangement of the blood-sinuses round about the lymphoid tissue is peculiarly favourable for the rapid escape of leucocytes into the general circulation. Although, for reasons already indicated, the circulation through the sinuses is probably very slow, the amount of blood entering and leaving the gland, judging from the size of the arteries and veins, must be considerable. Comparative observations on the blood entering and leaving the glands under different conditions would be of interest.

The function of the glands with reference to the red corpuscles is of much interest, and on this subject there is considerable diversity of opinion. W. F. Robertson suggests with due caution that one function of the glands is the manufacture of red blood corpuscles, and Clarkson, in a *Text-book of Histology*, 1896, states definitely, that "there seems little reason to doubt that they are local centres for the production of blood corpuscles, both red and white." Vincent and Harrison, on the other hand, hold that the glands are centres for the destruction of red corpuscles.

The theory that hæmolymp glands give rise to red blood corpuscles has been based on the presence in them of large cells containing in their interior pale bodies which, in some instances, stained with eosin. These have been supposed to be red corpuscles in process of formation. It has, in fact, been supposed that an intracellular process of red corpuscle formation was going on. The occasional presence in the glands of giant cells which I have seen in specimens from the sheep, from the rat, and from the dog, might be quoted in favour of this view by those who believe that these cells have something to do with the production of erythrocytes. But these cells are exceedingly rare in hæmolymp glands, having indeed hitherto escaped notice; and although they are abundant in the bone marrow where red corpuscles are being formed, it has not yet been proved that they have any real connection with this process. None of the ordinary stages of red blood formation, as this occurs in the bone marrow, have ever been seen in hæmolymp glands. Even in specimens obtained from embryos, I failed to find any nucleated red corpuscles, or any cells resembling

the nucleated predecessors of the red corpuscles in the bone marrow.

Intracellular formation of red corpuscles is a process which is described as occurring during embryonic life in various organs, but which is not recognised as occurring in the adult. But the red-corpuscle-containing cells which led Robertson and Clarkson to their views as to the function of the hæmolymp glands are abundant, sometimes extraordinarily abundant, in specimens from adult and old animals; they are comparatively scarce in young animals; while in embryonic life, so far as my own observations on specimens obtained from foetal sheep, calves, and rats go, they appear to be entirely absent. On the whole, there appears to be no evidence that the formation of red corpuscles is one of the functions of hæmolymp glands. The appearances that led Robertson and Clarkson to an opposite conclusion are capable of quite a different interpretation.

Cells containing red corpuscles in their interior can be found occasionally in the case of the sheep and bullock, commonly in the case of the rat, and very abundantly in the case of the dog. These cells, as has already been indicated, clearly belong to the leucocyte class, and my own observations amply confirm the opinion expressed by Vincent and Harrison, that they have taken up the red corpuscles into their interior by phagocytosis there to undergo disintegration. The appearances seen are not to be explained on any theory of intracellular formation of red corpuscles.

Various phases of disintegration can readily be made out. In the interior of the phagocytes the red corpuscles for a time may retain their normal appearance and staining reactions. Gradually, however, they swell slightly, and lose their property of staining with eosin, and at last appear like small vacuoles in the protoplasm of the phagocyte. These are commonly clustered round the nucleus, the peripheral part of the protoplasm being free from inclusions. Soon after this pigment begins to appear in the peripheral part of the protoplasm in the form of minute granules of a golden yellow colour. Whether the red corpuscles are completely digested, or whether any 'membrane' is extruded from the cells, it is difficult to say. Such extruded membranes are described by Vincent and Harrison. The

protoplasm of the phagocyte gradually becomes loaded with pigment. Many of these cells are provided with fine branching processes, and pigment may also be present in the interior of these processes. Much of the pigment that appears to be lying free in the sinuses is, in some specimens at any rate, really contained in such cell processes, which, however, may be very difficult to make out. The pigment thus deposited in fine granules appears, when it becomes very abundant, to run together as it were into large, irregular, homogeneous masses, which may almost entirely fill the protoplasm of the cell. Such masses of pigment, either contained in cells or free, may become so abundant as almost to block up some of the sinuses. Such sections present a very extraordinary appearance under the microscope, and even to the naked eye these parts of the section which correspond to the sinuses may have a distinct brownish-yellow tint. In some sections there are appearances that suggest that these masses of pigment may ultimately break down into excessively fine particles—particles which are individually scarcely visible under a  $\frac{1}{8}$  inch immersion lens—and that these may possibly be carried away from the gland.

Some facts in the structure of hæmolymp glands—in the case at any rate of the dog—seem to indicate that their function may be a cyclical one. This at any rate seems the most probable explanation of the fact that, in all parts of a single gland, the process of blood destruction may be at practically the same stage. This statement must not be taken too rigidly. It is certainly true that one can often easily make out divers phases of blood destruction in a single section, even side by side in a single sinus. In rare cases one can even make out blood corpuscles in different stages of disintegration within a single phagocyte. Still the fact remains that, on examining a section from a gland in which blood destruction is going on actively, one may find thousands of phagocytes present, and in a very large percentage of these some particular phase of corpuscle destruction will be present. For example, in a particular specimen one may find that the sinuses are filled with red corpuscles, amongst which are a considerable number of leucocytes, but careful search may fail to reveal a single cell with red corpuscles in its protoplasm. In another gland hyaline cells may be quite

numerous in the blood sinuses, and yet few or none of these may contain inclusions of any kind. Again, in another gland, the sinuses may be literally packed with large hyaline cells, practically all of which contain red corpuscles at about the same stage of disintegration. Again, in specimens where pigment is abundant, all the pigment may be in the form of small granules, or, on the other hand, the bulk of it may be in the form of the large irregular masses already described. These facts seem to indicate a cyclical function on the part of the glands—on the part, that is, of the individual glands. And this can hardly be explained as due to any general condition, seeing that different phases may be predominant in one animal in different glands found almost side by side. A partial explanation of these appearances may perhaps be found in a simple mechanical hypothesis. In certain hæmolymp glands there may be no sign of blood destruction going on at all. In others the process is found to be going on apparently with extraordinary energy in all the sinuses of the gland. What starts the process we do not know. But we may suppose that when once started the number of hyaline cells in the sinuses increases rapidly, and at the same time the individual hyaline cells attack and engulf the red corpuscles which are abundantly present. By this double process of increase in the number of hyaline cells, and increase in their individual size, the sinuses soon come to be completely blocked by them. Circulation through the sinuses is now at a standstill, or at any rate confined to a few minute capillary channels between the opposed hyaline cells. The process of phagocytosis is also practically at a standstill, because nearly all the red corpuscles in the sinuses have already been engulfed in the protoplasm of the phagocytes. If this process takes place with some degree of rapidity, one can understand how it is that we sometimes find a gland containing thousands of phagocytic cells in every section, every one of these containing apparently unaltered red blood corpuscles. And having got so far, we can also understand that the different phases in the disintegration of the red corpuscles, having begun together, will run a parallel course.

Attention has been directed to the differences which exist between the hæmolymp glands of the various species examined.

These seem to be mainly due to the difference in the activity with which the process of blood destruction is going on in the individual glands—at a minimum in those of the sheep and ox, at a maximum in those of the dog. And it may be suggested that this difference is associated with the number of hæmolymp glands present in the different species—numbered by hundreds in the sheep and ox, by units in the rat and dog.

Another important point of difference is found in the remarkable development of the arterial system in the hæmolymp glands of the dog. In a section from a gland only one-fourth of an inch in diameter, I have counted under a low power of the microscope over two dozen distinct arteries penetrating to all parts of the gland. In a similar section from a gland from the sheep, one would see only two or three small arteries near the hilus of the gland. Can any explanation of this fact be offered? Possibly the explanation may be found in the facts already noted concerning the extraordinary multiplication of phagocytic cells during the process of blood destruction. These cells increase in numbers and size until they almost block the sinuses of the gland, and it may be that the great development of the arterial system is associated with the difficulty under such circumstances of maintaining the circulation through the gland. It is interesting to note that in the case of the rat, where the process of blood destruction may be much more active than in the case of the sheep, but less active than in the dog, the arteries penetrate deeply into the gland, but are not developed to such a degree as are those of the dog.

#### SUMMARY.

Hæmolymp glands, while obviously closely related in their general structure to ordinary lymphatic glands, are not to be regarded as modifications of these, but as structures *sui generis*, differing from them as they do in their mode of development, in their distribution in the body, and in many details in their minute anatomy. Amongst these differences, the chief are the (usually) comparatively large size of the sinuses, the constant presence of blood in the sinuses, the frequent presence, some-

times in very large numbers, of large hyaline cells containing red corpuscles or pigment in their protoplasm.

There is no sufficient evidence that hæmolymp glands play any part in the formation of red blood corpuscles.

On the contrary, they appear to play a very active part in the destruction of red corpuscles and in the liberation of pigment. Pigment is frequently present in great abundance, even to the extent of blocking up some of the sinuses of the gland, and appears to be derived solely from the destruction of red corpuscles. The glands are also centres for the formation of white blood corpuscles, and the vascular arrangement of the glands is such as to favour the passage of white corpuscles into the general circulation.

In some respects the structure of hæmolymp glands agrees with that of the spleen. For example, in the occurrence of non-striped muscle in the capsule and trabeculæ, occasionally in the occurrence of lymphoid sheaths around the arteries, and in the occurrence of red blood corpuscle destruction. The process of blood destruction in the hæmolymp glands is, however, often far more active than is ever, so far as the writer can discover, found in the spleen. It is very likely that some of the bodies described as accessory spleens, are really hæmolymp glands.

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### EXPLANATION OF PLATES XXXI., XXXII.

Fig. 1. Hæmolymp gland of puppy three days old, to show general arrangement. Zeiss, oc. 2, obj. A. *C*, capsule; *P.S.*, peripheral sinus; *C.S.*, central sinuses; *H.C.*, nuclei of the hyaline leucocytes, which in this particular specimen were very abundant in all the sinuses (see fig. 4). Note the dense peripheral layer of lymphoid tissue, and the indication, near *C*, of the formation of a germ centre.

Fig. 2. Hæmolymp gland of foetal sheep. Zeiss, oc. 2, obj. D. *F.C.*, fat cells outside capsule; *P.S.*, peripheral sinus; *S*, ill-defined central sinus; *L.T.*, lymphoid tissue; *r.b.c.*, red blood corpuscles. The lymphoid tissue is not densely packed with leucocytes. The peripheral sinus is distinctly marked off from the lymphoid tissue, but the central sinuses are represented merely by indefinite spaces filled with red corpuscles among the leucocytes of the lymphoid tissue. Leucocytes are abundant in the blood in the sinuses.

Fig. 3. Hæmolymp gland of puppy three days old (a different specimen from fig. 1). Imm.  $\frac{1}{8}$  in. *L.T.*, lymphoid tissue (the nuclei of the leucocytes are represented diagrammatically); *H.C.*, hyaline cells; *r.b.c.*, red blood corpuscles. The section shows a comparatively large number of hyaline cells in the blood sinus.

Fig. 4. A portion of the section shown in fig. 1, highly magnified. Imm.  $\frac{1}{8}$  in. The sinus is almost completely filled with hyaline cells. Red corpuscles are scanty.

Fig. 5. Hæmolymp gland from an old retriever dog. Imm.  $\frac{1}{8}$  in. The figure shows a portion of a sinus containing numerous hyaline cells (*H.C.*), with red corpuscles in their interior (in the specimen practically all of these were stained deeply with eosin), and leucocytes, *r.b.c.*, red blood corpuscles, and *G.P.*, granular pigment (intra-cellular).

Fig. 6. Hæmolymp gland from an old dog. Imm.  $\frac{1}{8}$  in. *P.*, pigment masses; *G.P.*, granular pigment; other letters as above. The figure indicates the abundance of pigment common in specimens obtained from the dog. At *H.C.*<sub>2</sub> a hyaline cell loaded with pigment is seen. Many of the other large masses of pigment correspond to hyaline cells. Apparently the cells ultimately die, and the pigment masses break down. In this specimen hyaline cells loaded with pigment were abundant throughout the section; hyaline cells

containing red corpuscles were very scanty. Masses of pigment are present in the lymphoid tissue as well as in the sinuses.

The figures were all outlined by means of the camera lucida. Only the nuclei of the lymphocytes are represented.

MICRO-PHOTOGRAPHS. (PLATE XXXIII.)

1. Portion of a sheep's gland, showing the fibrous reticulum, blackened (Cox's modification of Golgi's method). Zeiss D.

2. Portion of hæmolymp gland of rat showing a small artery giving off a branch in the midst of the lymphoid tissue. Zeiss D.

**Dr DRUMMOND on the Structure and Functions of Hæmoglymph Glands.**

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Microphoto 2.

Microphoto 1.





NOTE ON THE PRESENCE OF CILIATED CELLS IN THE  
HUMAN ADULT KIDNEY. By F. WACE CARLIER, M.D.,  
B.Sc., *Professor of Physiology in the Mason College, Bir-*  
*mingham.*

THAT the cells lining the convoluted tubules bear cilia in most mammals has been recognised for a considerable time by continental writers, and has been recently reinvestigated by me. My results will be found published in *The Veterinarian*, vol. lxxii. p. 466. In that paper I pointed out the occurrence of ciliated cells throughout the convoluted and spiral tubules of the kidney in most of the domestic animals.

Quite recently I was fortunate enough to obtain a perfectly healthy adult human kidney from the post-mortem room of the Edinburgh Royal Infirmary, and am now in a position to state that the human kidney forms no exception to the rule that obtains in the case of the lower mammals.

Cilia have indeed been observed in the human adult kidney by Lebedeff (1), Marchand (2), Langhans (3), Werner (4), and Oértel (5), who studied the organ from a pathological point of view, and all of them consider the ciliated appearance to be due to some pathological change, and not at all referable to the normal condition.

*Method.*—The kidney, which was quite fresh when obtained, was cut into small pieces and placed in Müller's fluid and spirit to harden. This fluid is unfortunately not a very good fixative, as the tissues tend, if not very carefully handled, to shrink somewhat in the subsequent process of embedding in paraffin.

Sections of the thickness of  $4\ \mu$  were cut on the Cambridge rocking microtome, fixed to albumin-coated slides after spreading on water, and on removal of the paraffin with xylol and alcohol were stained in Heidenhain's iron-alum hæmatoxylin (long method), or in hæmatoxylin, rubin, and orange, or in methyl-blue eosine mixture, Mann's formula. They were examined with the aid of a Leitz  $\frac{1}{2}$  oil immersion objective

SYMMETRICAL PERFORATIONS OF THE PARIETAL BONES: INCLUDING AN ACCOUNT OF A PERFORATED AND DISTORTED CRANIUM FROM THE LIVERPOOL MUSEUM. By A. M. PATERSON, M.D., *Professor of Anatomy*; and F. T. LOVEGROVE, M.R.C.S. Eng., *Robert Gee Fellow in Anatomy, University College, Liverpool.* (PLATES XXXVI.-XXXIX.)

THE following is an account of three cases of double symmetrical perforations of the parietal bones, the most remarkable of them in a microcephalic and distorted cranium kindly sent by Dr H. O. Forbes, Director of the Liverpool Museums, to the Anatomical Department of University College for examination.

I. THE CRANIUM.

The specimen (Pl. XXXVI. and XXXVII. figs. 1-4) consists of cranium only. It is scaphocephalic and microcephalic: the sutures are obliterated, and in each parietal bone behind the vertex is a symmetrical perforation of large size.

Viewed *from above* (fig. 1) the sutures are seen to be obliterated (except the lambdoidal suture, which is faintly indicated on the left side). The parietal region is symmetrically vaulted. In each parietal bone at its posterior superior angle is a large perforation, symmetrically placed, and separated in the middle line by a bridge of bone without sutures, 20 mm. broad at the narrowest part. The *left* perforation reaches the lambdoidal suture, which is faintly marked in the surface of the skull. It is oval in outline, and measures 4.0 cm. antero-posteriorly: 3.2 cm. from side to side. The *right* perforation is smaller and more circular, and does not extend so far forwards or backwards. It measures 3.0 cm. from before backwards; 3.2 cm. from side to side. The margins of both holes are bevelled externally, and (to a less extent) internally, and the outer surface of each is marked by numerous diverging striations.

A *front view* of the cranium (fig. 2) shows the exaggerated vault of the frontal bone, temporal ridges well marked, and curved in such a way as to narrow the forehead to a remarkable degree (62 mm.): prominent external angular processes, and well marked but small supra-orbital arches. The frontal bone is flattened in its lowest part, and becomes vaulted above. In its centre is a prominent ridge,

tubule are dome-shaped and of comparatively large size; their lateral outlines are well marked, as can be seen in the figure, but Heidenhain's rods are absent, the cytoplasmic granules being quite irregularly arranged throughout the cell, though joined together by fine threads. The cilia, including the thin basal pieces, measure  $3.1\ \mu$  in length. The nuclei are situated close to the basement membrane.

The human kidney, therefore, comes in the series alongside that of the mouse, as far as regards the length of the cilia, and, as in the mouse, the cilia do not differ appreciably in length in the convoluted and spiral tubules.

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A NOTE ON THE THYMUS GLAND IN THE KOALA  
(*PHASCOLARCTUS CINEREUS*). By JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's College, Belfast.*  
(PLATES XXXIV., XXXV.)

AT a meeting of the Anatomical Society, held in November 1897, I read a paper on "The Thymus Gland in the Marsupialia," and exhibited photographs of dissections and of microscopic sections of this organ. This communication appeared in the *Journal of Anatomy and Physiology* for January 1898. The main object of my paper was to show that in various marsupials two well-developed lobes, having a typical thymus structure, are situated in the ventral portion of the neck, immediately beneath the skin and platysma, and superficial to the sterno-mastoid muscles and the depressors of the hyoid bone. These thymus bodies had previously been entirely overlooked or mistaken for salivary or lymphatic glands. The material at my disposal, although fairly extensive, did not include representatives of several groups of marsupials, and, at the suggestion of Professor G. B. Howes, additional observations on the anatomy of the marsupial thymus were made in his laboratory by Mr James Johnstone. The results of this investigation appeared in the *Journal of the Linnean Society—Zoology*, vol. xxvi.

I found the subcutaneous cervical thymus in animals belonging to each of the three families of the diprotodont division of the marsupialia, but in none of the polyprotodonts that I examined. Mr James Johnstone confirmed and extended my observations, but in two young specimens of the koala his results were not such as might have been anticipated. In neither of these animals could he find any trace of a thymus, either in the neck or in the thorax. When working at this subject I had no opportunity of examining a koala, but as this animal is closely related to the vulpine phalanger and to the wombat, in both of which I found the superficial cervical thymus well developed and persisting until adult life, its constant absence in the koala was so improbable as to suggest the propriety of further observations. Through the kindness





running upwards as far as the bregma. The supraciliary ridges are faintly indicated. About 25 mm. from the glabella on the left side of the middle line is a small round hole communicating with the left frontal sinus. It appears to have been formed during life, as attached on each side of it is a small irregular spicule of bone.

*A side view* (fig. 3) shows the remarkable expansion of the parietal and occipital regions as compared with the frontal and temporal regions. The slope of the frontal bone is well marked; the temporal fossa is small and shallow, and the root of the zygoma is separated from the external angular process of the frontal bone by a distance of only 40 mm. The temporal ridge is well marked in front and behind, but is only faintly indicated in its middle third. On the right side the greater part of the great wing of the sphenoid bone is wanting. On both sides its articulations with the frontal and the squamous portion of the temporal bone are clearly indicated. It does not appear to articulate with the parietal bone. The mastoid processes are small and infantile in character; and below do not reach to the level of the occipital condyles. The digastric grooves are well marked.

*From behind* (fig. 4) the vaulted character of the cranium is well seen. The external occipital protuberance is prominent. The region above it is raised in an exaggerated dome-like form; the part below it is of large extent, flattened, and directed downwards and backwards. The sutures are practically obliterated, and the whole of the surface shows an erosion of the outer table of the skull, particularly over the upper portion on the left side.

*The inferior surface* (figs. 7 and 8) shows the remarkably short length of the basi-cranial axis of the skull, between the foramen magnum and the glabella (97 mm.) as compared with the total length of the cranium (178 mm.). Only the cranial bones are present. The area for attachment of the facial bones is extremely small, corresponding to the narrow forehead, shallow and small temporal fossæ, and infantile mastoid processes. The occipital condyles are flat, small, and asymmetrical, and their long axes are more transverse than usual. The foramen magnum is normal in size, but irregular and asymmetrical in shape. Around its margin posteriorly between each condyle is a slightly elevated ridge of bone. In front of each condyle is a similar more prominent bar of bone ending anteriorly in a free knob-like extremity, not united to the neighbouring piece. The series, together with the condyles, have a likeness to the under surface of an atlas, the anterior arches of which have not joined together.

*The interior of the cranium* can be examined by the light afforded by the parietal perforations. A very remarkable condition is found in the basal fossæ. The posterior fossa is large and capacious. It occupies more than two-thirds of the base of the cranium, and is covered by the greater part of the vault. The middle and anterior fossæ are very small. Both are perforated and excavated by holes and depressions of various size, and are separated by the lesser wings of the sphenoid bone, which are distorted by the formation of osseous plates erected on their upper surfaces, so

as to still further deepen and narrow the anterior fossa. The floor of this fossa is sloped towards the median line and is convex; it is remarkably deep over the cribriform plate, which is concave in the antero-posterior direction. The pituitary fossa is well marked. The anterior and middle fossæ are roofed over by the narrow, sloping frontal bone, which still more limits the capacity of this part of the cranium. All the fossæ are enlarged at the expense of the bones in the base of the skull. Both basi-sphenoid and basi-occipital bones are much thinner than usual. In the posterior fossa an abnormal arrangement of the *venous sinuses* was seen to have existed. On the left side the lateral sulcus is absent, except close to the jugular foramen. Instead, there is a well marked groove in the position of the occipital sinus, extending from the internal occipital protuberance to the foramen magnum, and along its margin to the jugular foramen of the left side. Here it is joined by a deep groove half an inch in length, corresponding to the terminal portion of the lateral sulcus. On the right side the lateral sulcus has its usual form and course.

*Measurements.*

The measurements were difficult to obtain, as the obliteration of sutures left the determination of the standard points doubtful.

*Cranial capacity*, 1225 c.c. (measured with mustard seed).

| <i>Measurements—</i>              |         | <i>Measurements—continued.</i>          |           |
|-----------------------------------|---------|---|-----------|
| Maximum length . . . . .          | 178 mm. | Breadth of foramen magnum . . . . .     | 26 mm.    |
| Ophryo-iniac length . . . . .     | 149 mm. | Minimum inter-orbital breadth . . . . . | 16 mm.    |
| Ophryo-occipital length . . . . . | 166 mm. | <i>Arcs</i> —Frontal . . . . .          | 112 mm.   |
| Maximum breadth . . . . .         | 124 mm. | Parietal . . . . .                      | 80 mm.    |
| Biasterial breadth . . . . .      | 105 mm. | Occipital, superior . . . . .           | 128 mm.   |
| Minimum frontal breadth . . . . . | 62 mm.  | Occipital, inferior . . . . .           | 61 mm.    |
| Bistephanic breadth . . . . .     | 103 mm. | Horizontal circumference . . . . .      | 456 mm.   |
| Biauricular breadth . . . . .     | 79 mm.  |   |           |
| Bizygomatic breadth . . . . .     | 103 mm. | <i>Indices—</i>                         |           |
| Basi-nasal length . . . . .       | 80 mm.  | Cephalic . . . . .                      | — 69·66   |
| Basi-bregmatic length . . . . .   | 128 mm. | Vertical . . . . .                      | — 71·91   |
| Basion-obelion length . . . . .   | 153 mm. | Breadth height . . . . .                | — 103·225 |
| Basion-lambda length . . . . .    | 150 mm. | Frontal . . . . .                       | — 60 19   |
| Basion-iniac length . . . . .     | 66 mm.  |   |           |
| Basion to opisthion . . . . .     | 33 mm.  |   |           |

II. AND III. CALVARIA IN THE PATHOLOGICAL MUSEUM OF UNIVERSITY COLLEGE, LIVERPOOL.

Among the osteological series in the Pathological Museum we have found two calvaria, with symmetrical perforations of the parietal bones. There is no history attached to the specimens.



of Dr Glegg Wilson, who sent me a young koala from his collection of Australian animals, I have been able to make a dissection of another specimen. Both Johnstone's specimens measured about 20 cm. from the snout to the root of the tail; mine was larger, but not full grown. It was about 30 cm. long, and its hairy covering was well developed. On reflecting the skin of the neck two thymic lobes were exposed (Pl. XXXIV.). They were in close contact with one another in the median plane, the right lobe slightly overlapping the left one. Each lobe was about 15 mm. long, 12 mm. broad, and on an average nearly 3 mm. thick. Anteriorly, it touched and partly concealed the corresponding gland. Its posterior border was 15 mm. distant from the manubrium sterni. On microscopic examination the larger lobules showed a division into cortical and medullary substance, and the latter contained a number of Hassall's corpuscles.

The thorax was opened, and a careful dissection made of its contents to discover, if possible, a thymus, or its remains. A small quantity of fatty-looking tissue was found in the anterior mediastinum, near the usual position for a thoracic thymus. It was removed, embedded in paraffin, and the entire piece cut up, but no trace of thymus tissue could be discovered. The mass consisted simply of fat cells and ordinary connective tissue.

The results obtained from the examination of this animal agree with those of Mr Johnstone, so far as the thoracic thymus is concerned. In none of the three specimens examined could it be found. In all probability it atrophies at an early period.

The superficial cervical thymus was found in my specimen with the greatest ease, while in Johnstone's two cases a careful examination by one familiar with its appearance in other marsupials gave a negative result. Mr Johnstone, in his paper, suggests that, as his specimens of the koala were young, he may possibly have overlooked the presence of a small rudiment of a thymus, which would have developed later in life.

The rate of growth, and the time of disappearance of the thymus, is well known to differ greatly in different animals, and even in the same animal, under varying conditions. In the case of the koala, a study of the development and atrophy of the thymus ought to yield interesting results.

**SYMMETRICAL PERFORATIONS OF THE PARIETAL BONES: INCLUDING AN ACCOUNT OF A PERFORATED AND DISTORTED CRANIUM FROM THE LIVERPOOL MUSEUM.** By A. M. PATERSON, M.D., *Professor of Anatomy*; and F. T. LOVEGROVE, M.R.C.S. Eng., *Robert Gee Fellow in Anatomy, University College, Liverpool.* (PLATES XXXVI.-XXXIX.)

THE following is an account of three cases of double symmetrical perforations of the parietal bones, the most remarkable of them in a microcephalic and distorted cranium kindly sent by Dr H. O. Forbes, Director of the Liverpool Museums, to the Anatomical Department of University College for examination.

I. THE CRANIUM.

The specimen (Pl. XXXVI. and XXXVII. figs. 1-4) consists of cranium only. It is scaphocephalic and microcephalic: the sutures are obliterated, and in each parietal bone behind the vertex is a symmetrical perforation of large size.

Viewed *from above* (fig. 1) the sutures are seen to be obliterated (except the lambdoidal suture, which is faintly indicated on the left side). The parietal region is symmetrically vaulted. In each parietal bone at its posterior superior angle is a large perforation, symmetrically placed, and separated in the middle line by a bridge of bone without sutures, 20 mm. broad at the narrowest part. The *left* perforation reaches the lambdoidal suture, which is faintly marked in the surface of the skull. It is oval in outline, and measures 4.0 cm. antero-posteriorly: 3.2 cm. from side to side. The *right* perforation is smaller and more circular, and does not extend so far forwards or backwards. It measures 3.0 cm. from before backwards; 3.2 cm. from side to side. The margins of both holes are bevelled externally, and (to a less extent) internally, and the outer surface of each is marked by numerous diverging striations.

A *front view* of the cranium (fig. 2) shows the exaggerated vault of the frontal bone, temporal ridges well marked, and curved in such a way as to narrow the forehead to a remarkable degree (62 mm.): prominent external angular processes, and well marked but small supra-orbital arches. The frontal bone is flattened in its lowest part, and becomes vaulted above. In its centre is a prominent ridge,

No. 306 (Pl. XXXVIII. fig. 5) is a calvarium sawn off above the lambda. The coronal suture is well marked, and there is a metopic suture. The sagittal suture is visible, except for about 25 mm. near its posterior end. In each parietal bone there is a perforation separated across the middle line by a bridge of bone 19.75 mm. in its narrowest part. The sagittal suture is obliterated in relation to this bridge of bone, which is grooved on its under surface for the superior longitudinal sinus. Across the middle line, and connecting the two perforations, is a transverse suture passing through the thickness of the bone. The perforations of the parietal bones are neither large nor equal in size. The right hole is somewhat triangular in shape, the apex pointing outwards. It measures 17 mm. transversely, and 8.5 mm. from before backwards. The left hole is smaller and rhomboidal in shape; it measures 11 mm. from side to side, and 7 mm. antero-posteriorly. The margins of both holes are bevelled, and are marked externally by faint striations. Internally, grooves for meningeal vessels can be traced to the perforations.

No. 307 (fig. 6) is a similar calvarium sawn through above the level of the lambdoidal suture. The coronal suture is well marked, and the sagittal suture is obliterated for 25 mm. in the neighbourhood of the parietal perforations.

In this specimen the parietal holes communicate across the middle line, presenting an hour-glass form. They are symmetrical and almost circular. The narrow interval between them measures 3.75 mm. from before backwards. The lateral portions measure from before backwards 16 mm. on the right side, 17.75 mm. on the left side, and the total transverse diameter of the two holes together is (R. 21, L. 16) 37 mm. The margins of the perforations are bevelled both externally and internally. Internally grooves corresponding to meningeal vessels run to the margin of the holes. The longitudinal sulcus deviates from the middle line so as to end in front of the left perforation. It begins again in the middle line behind the perforations.

Two points of interest are noticeable in the above specimens: (1) the distortion and microcephaly of the cranium (L), and (2) the presence of parietal perforations.

(1) The microcephalic character of the skull is not excessive, its capacity being 1225 c.c. The distortion consists in a greatly expanded vault superiorly and posteriorly, associated with arrest of development of the base of the cranium, and obliteration of the cranial sutures. The effect of closure of the sutures is apparent not only in the expansion of the vault of the cranium, but also in the forcing downwards of the base of the skull in front of the foramen magnum, and the consequent deepening of the basal fossæ. Associated characters are the imperfect condition of the foramen magnum; the infantile condition

of the mastoid processes, and the character of the occipital condyles.

In fig. 7, the contour of the cranium (*c*) is compared with the contours of the normal Irish skull (*a*) and the skull of the microcephalic idiot (*b*), as described by Cunningham and Telford Smith. The differences are seen to be due to the small size of the basi-cranial axis, and the projection of the vault of

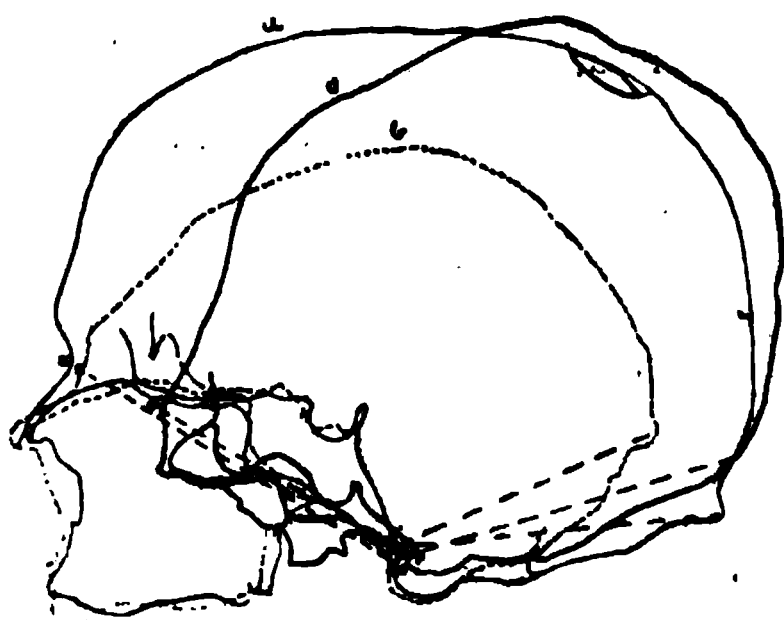


FIG. 7.—Liverpool cranium (Case I.) (*c*) compared with normal Irish cranium (*a*) and that of a microcephalic idiot (*b*), as figured by Cunningham and Telford Smith (\* . . . . \* = Basi-cranial Axis).

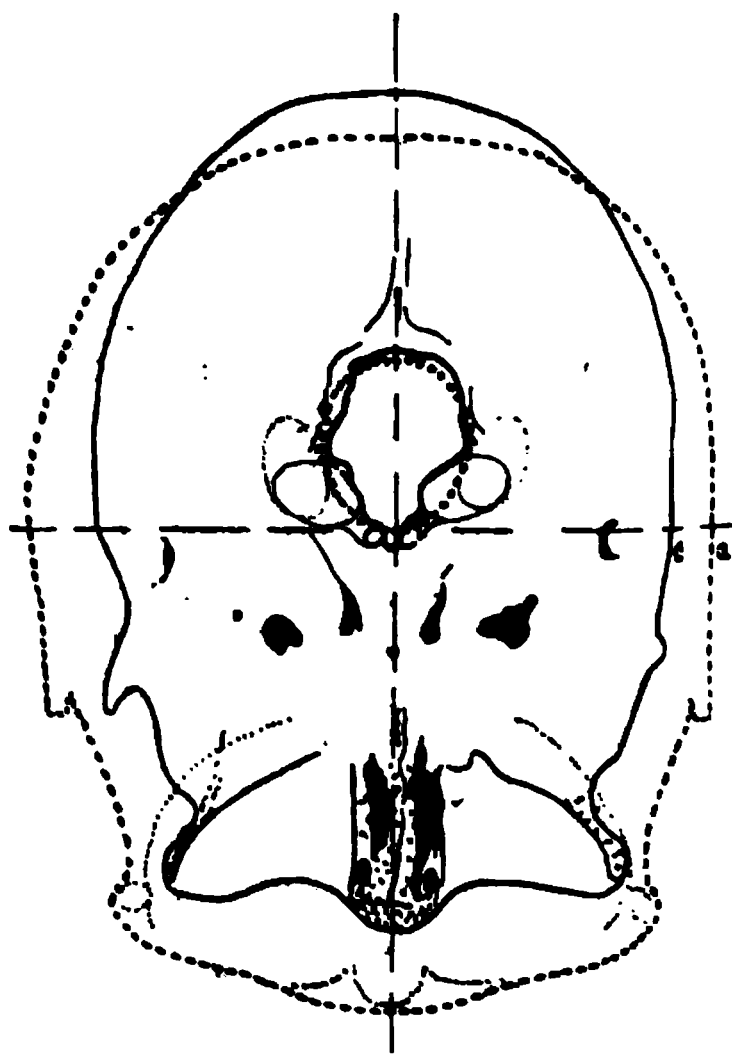


FIG. 8.—Base of Liverpool cranium (*c*) compared with the average of two normal European crania (*a*).

the cranium. In fig. 8 a similar comparison is made of the basal outline of the cranium (*c*) with the average of two normal European crania (*a*).

We have been struck with the general resemblance which this cranium in its upper part has to the Neanderthal skull, and the fragment described by Dubois from Java. If this cranium had been without its under surface, it would have been in general contour very similar to these two specimens.

(2) *Parietal Perforation*.—Humphry (6) is the first English author to refer to symmetrical perforations. He mentions a

cranium in the Cambridge Anatomical Museum, possessing parietal perforations which admitted "the end of the finger."

The first case fully described in 1865 was by Sir William Turner (2), from a specimen obtained by Dr T. J. MacLagan and illustrated by Dr Richard Caton. It was very similar to the specimens described above; there was a suture connecting the left perforation with the lambda, and the holes were filled up by cribriform membranes. They were situated at the postero-superior angles of the parietal bones, and there was an additional perforation in the median line in the supra-occipital bone. The sagittal suture was partially obliterated.

In all, ten cases of parietal perforations have been previously recorded. Besides Humphry's and Turner's examples, Wrany (3) has recorded four cases; Broca (4) is responsible for three, and D. M. Greig (7), formerly Demonstrator of Anatomy in University College, Dundee, has described one case.

Of Wrany's four cases (3) one appears to be an example of mere enlargement of the normal parietal foramen, the left being the larger of the two perforations and big enough to admit a raven's quill. Of Broca's cases, one, a negro cranium (5), is also an example of an enlarged parietal foramen. Greig's case is particularly interesting from the fact that the subject is a soldier who was alive at the beginning of the year (8). The condition in this case is known to be congenital. The pulsation of the brain can be felt beneath the perforations, and the scalp is freely movable over them.

With the three examples described above, we are acquainted altogether with eleven certain, and thirteen possible examples of double parietal perforations. They present, taken together, three points more or less in common: (1) the position of the perforations in the position of the normal parietal foramen at the postero-superior angles of the parietal bones; (2) the microcephalic character of the cranium, referred to in four cases—Turner's, one of Broca's (Baron Larrey's case), Greig's case, and the cranium from the Liverpool Museum; and (3) the partial or complete obliteration of sutures referred to in five cases—three Liverpool cases, Turner's, and one of Wrany's cases.

The differences among the several cases are mainly differences in size, the holes varying from mere enlargement of the parietal

foramen to perforations measuring, as in one of our cases, 4·0 by 3·2 and 3·2 by 3 cm.

*Possibility of Trephining.*—We should not enter into the question of the possibility of trephining having occurred in one of our specimens, had not the cranium been figured in Dr Robert Munro's *Prehistoric Problems*, 1897 (13), and cited as the solitary example of double trepanning known in an English skull. The "trepanned apertures show clean cut and slightly round edges . . . , the production of which seems to me to have entailed the use of surgical instruments of a higher order than were to be had either in the Bronze or Stone Age." As the deformity of the skull "was probably due to pathological causes, it is interesting to note that the operation (of trepanning) had been resorted to as a means of treatment."

Broca, who was among the first anthropologists who investigated the occurrence of artificial perforations of the cranium, clearly recognises the difference between such holes and the congenital symmetrical double perforations of the parietal bones, of which the cranium in question is in our opinion an undoubted example. The cranium was found in the churchyard at Eastry, near Sandwich, and the inference is that it is at any rate not prehistoric. There is no evidence of inflammatory change in the neighbourhood of the perforations; in short, the position, and the symmetrical nature of the foramina, associated with other similar instances, one diagnosed during life and known to be congenital, along with the evidence (positive and negative) derived from an examination of the perforations themselves, compel us to dismiss at once the view of their formation suggested by Dr Munro, and to place the perforations in this cranium among those of congenital origin.

*Relation to Parietal Depressions.*—It does not appear as if parietal perforations were related in any way to the symmetrical parietal depressions recorded by Humphry (6), Shepherd (9), and others (10). The latter appear to be congenital depressions in some cases, though they are regarded by Shepherd as due frequently to senile changes in the temporal artery. They are due to a deficiency in the outer table; and the inner table is not affected. The normal parietal foramina may be present along with them, and the examples recorded do not agree in

position with the situation of parietal perforations, being situated further forward on the bones.

*Relation to the Parietal Foramina.*—The situation of parietal perforations in relation to that of the normal parietal foramina has led to the very natural suggestion by Turner, Humphry, and others, that the perforation is due to an alteration in vascular conditions, an enlargement in size of meningeal vessels, or an increase in the number of vessels in the position of the parietal foramina.

Broca (4) indeed regards the parietal foramina themselves as abnormal. While they are not an essential characteristic of the mammalian parietal bone as a rule—we have only found them in a bear, an ox, and a leopard among the skulls in our possession—there can be no doubt that they are a normal occurrence in the human parietal bone. Out of 204 adult parietal bones examined, we have found the foramina present in 66 per cent., absent in 33 per cent., and present as a single median hole in 1 per cent.

At the same time it is difficult to understand how even a considerable vascular disturbance, such as a blood island or a *circulus venosus*, much less a mere emissary vein or meningeal artery, could account for perforations of the size of those recorded.

With the object of ascertaining if the arrangement of the diploic veins in normal crania would throw any light on the conditions, we have filed off the outer table of the skull from five crania. In the cases examined the arrangement was fairly regular throughout. A large posterior temporal vein collects from the upper part of the parietal bone, and communicates in some cases with the occipital vein. In one case a '*circulus venosus*' was present (but not in the position of the perforations), but the bone was as well ossified within the circle as elsewhere.

*Ossification of the Parietal Bones.*—The examination of ossifying parietal bones throws some light upon the formation of foramina, depressions, and perforations. In all our specimens of foetal parietal bones, there was only one example of apparent ossification from more than one centre. In a three months' embryo the bone formation is occurring in two separate areas which are joined together, however, along a line which passes



foramen to perforations measuring, as in one of our cases, 4·0 by 3·2 and 3·2 by 3 cm.

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*Ossification of the Parietal Bones.*—The examination of ossifying parietal bones throws some light upon the formation of foramina, depressions, and perforations. In all our specimens of foetal parietal bones, there was only one example of apparent ossification from more than one centre. In a three months' embryo the bone formation is occurring in two separate areas which are joined together, however, along a line which passes

vertically down the centre of the bone. The examination of eighty-five parietal bones in nine months' foetuses shows the existence of a very constant cleft in the upper border of the bone, in the position of the parietal foramen, formed by a vessel which produces a rounded or oval notch (fig. 10) at the outer angle of the cleft. This cleft is present in seventy specimens. In fifteen cases it is absent or indistinguishable from the numerous small serrations along the upper border of the bone.

The presence of this emissary vessel is thus able to retard the bone formation in the situation of the parietal foramen. In six cases out of the eighty-five, there were remarkable thinnings, even (in two cases) perforations in the parietal bones, placed symmetrically in one or more situations (Pl. XXXIX. figs. 9, 10, 11). When present, these perforations are oval in form, are due to excessive thinning of the bone, are symmetrically placed, and not always in the same position. They may be present along with thinnings of the bones, and along with the clefts representing parietal foramina. They do not occur in the exact situation of the parietal foramen. When the bone is thinner than usual, it has a cribriform character.

Both thinnings and perforations in the foetal bones look exactly as if, owing to inequality of growth in the cranium and cerebrum, pressure had been exerted upon the ossifying parietal bones by the subjacent cerebral convolutions. But the usual parietal perforations occur in the situation of the normal parietal foramina. It has been shown that the existence of the usual vessel or vessels in the ordinary course of events retards the bone formation. It is conceivable that in certain cases, it may be along with larger or more numerous vessels, the same inequality of growth and consequent pressure of the cerebral convolutions may keep open and enlarge this embryonic cleft, and so give rise to the large perforations present in some few cases. In one of our cases there is coalescence of the perforations across the middle line; and in another a suture connects them together. The idea of such a cause being responsible is supported by the fact that in several of the examples recorded the cranium has a microcephalic character, or there is partial or complete obliteration of the cranial sutures.

One is inclined, therefore, to causally associate the general con-

**Professor PARERSON on Symmetrical Perforations of the Parietal Bones.**

**FIG. 1.**

**FIG. 2.**





FIG. 8.



FIG. 5.

FIG. 6.





FIG. 9.

FIG. 10.

FIG. 11.



dition of the cranium described, arrest of development of the base, closure of sutures, and microcephalic character, with the existence of these enormous perforations of the parietal bones.

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### EXPLANATION OF PLATES XXXVI.-XXXIX.

Figs. 1-4. Superior, anterior, lateral, and posterior views of the cranium (Case I.).

Figs. 5, 6. Calvaria from Pathological Museum (Cases II. and III.).

Figs. 9, 10, 11. Parietal bones of nine months' fetuses—perforated and thinned.

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THE CAUSES OF THE ENTRANCE OF OXYGEN INTO  
THE BLOOD IN THE LUNGS. By J. J. CHARLES, M.D.,  
F.R.S.E., *Professor of Anatomy and Physiology, Queen's  
College, Cork.*<sup>1</sup>

THE causes of the entrance of oxygen into the blood in the lungs is a subject on which much difference of opinion exists. In any consideration of this question, at least three factors must be considered, namely: diffusion, the chemical affinity of hæmoglobin, and the secretory activity of the endothelium. The two rival views are: (1) the so-called diffusion theory in which the chemical affinity of hæmoglobin is included, and (2) the vitalistic theory, in which the secretion of oxygen by the endothelium plays an important part, in addition to diffusion and the chemical affinity of hæmoglobin.

I. Diffusion at the lungs is a physical process whereby oxygen tends to pass from a point of higher to one of lower tension—that is, from the air through the moist membranes into the blood. Of course, as Haldane has remarked, “the passage of oxygen molecules inwards will be equally fast, whether the hæmoglobin is saturated or not; only when the latter is saturated, the oxygen would be passing equally fast out again, if the process were one of diffusion only.” Many accepting the results of Pflüger and others with the aërotonometer and the gas pump, maintain that the tension of the oxygen in the air of the air-cells is greater than in the blood in the lungs, and consequently that this gas passes inwards in accordance with the laws of diffusion. (See Appendix.) But Bohr (1) is entirely at variance with Pflüger; for experimenting with the hæmataërometer—a modification of the aërotonometer—he concluded that the tension of the oxygen in the arterial blood is, as a rule, greater than in the air in the trachea, though it must be admitted that his experiments were

<sup>1</sup> This paper was read at the opening of a discussion on this subject, in the Section of Anatomy and Physiology, *British Medical Association*, Portsmouth, 1899.

so adversely criticised by Hufner and Fredericq that for a long time little attention was paid to them. But the recent investigations of Haldane and Lorrain Smith (2) support the conclusions of Bohr; and as their investigations form an important element in this inquiry, it is right that they should be considered somewhat in detail. These observers have experimented on man and other animals, and they cause them to respire air containing a small amount of carbonic oxide, until the percentage saturation of hæmoglobin with that gas becomes constant. In the case of man, they take from his finger a definite quantity<sup>1</sup> of blood, and determine by titration with carmine, the percentage saturation of the hæmoglobin in it with carbonic oxide. And as the final saturation of the hæmoglobin with carbonic oxide is due to the relative tensions of the carbonic oxide and oxygen in the blood, they are able to calculate its oxygen tension, once they have ascertained its carbonic oxide tension. They have found the oxygen tension in the arterial blood of man to be 38·5 per cent. of an atmosphere,<sup>2</sup> the tension in the dog to be 17·6 to 24 per cent., and in birds 44 per cent.—that is, considerably higher than the oxygen tension of the air in the alveoli, which is calculated to be about 13 per cent. of an atmosphere (= 99 mm. Hg.) in man, and is probably the same in most of the higher animals. These results differ widely from those obtained by all previous observers except Bohr, the tension of the oxygen of the arterial blood of the dog having been ascertained by Fredericq to be only 12 to 14 per cent. of an atmosphere, instead of 21 per cent. as made out by the carbonic oxide or colorimetric method.

Many objections, however, have been raised, not only to the method pursued by Haldane and Smith, but to the inferences they have drawn from their experiments. Thus it was pointed out, even by themselves, that the dissociation of oxyhæmoglobin takes place more readily with a weak solution than with a strong one, and that carbonic oxide hæmoglobin is to a certain extent dissociated by sunlight. To meet these objections they have made test experiments, by which they have been able to apply corrections to their results, so that they are now convinced

<sup>1</sup> I understand that lately they do not measure the quantity.

<sup>2</sup> In their early experiments they made the oxygen tension in man to be 26·2 per cent. = 200 mm. Hg.

of their accuracy. Some authorities, however, are still disposed to look with suspicion on results which require so many corrections.

It has also been suggested that, in the experiments of Haldane and Smith, the hæmoglobin might be decomposed or be in the state of methæmoglobin; but this change, even if it occurred, could have little effect on the result. There is the further possibility that a fall of the temperature of the body might occur during the experiment, and this, as Lorrain Smith suggests, by paralysing the mechanism of absorption (the secretory activity of the alveolar endothelium), would reduce the oxygen tension of the arterial blood; but they have taken this fully into consideration, and in some cases have kept the animal, such as a mouse, in a vessel placed in a warm bath at 25° to 30° C.

Again it might be urged that the small quantity of blood employed in these experiments is not a fair or average sample of the blood in the body—at least, not as reliable as the large quantity used in the aërotonometer method. It is alleged, too, that as it has been shown that the percentage of red corpuscles and of hæmoglobin in the blood varies in different parts of the body, and that the percentage of corpuscles in a part is altered by posture (3), the result would be influenced thereby in both instances. Again, it is said that if a portion of the lung should not be ventilated at all, or only partially, as is known sometimes to occur, the blood would absorb more carbonic oxide than ordinarily, and the results would, therefore, be inaccurate. In reply to these various objections, I may state that I have learned that Haldane and Smith now make use of a larger amount of blood (50 c. mm.) in their experiments than they originally did, and that as each of these lasts, on an average, 15 minutes, there is ample time for complete mixture of the blood from different parts of the body to take place.

The alleged discovery of carbonic oxide in normal blood by Nicloux seems at first sight a serious objection. But the test employed for the detection of carbonic oxide is not accepted by chemists as reliable; and, even if it were, the amount of this gas in blood, according to St Martin (4), is about 1·5 c.c. in a litre—that is, only ·15 per cent.; whereas, during the experiments of Haldane and Smith, the blood is from 30 to 80 per cent.

saturated with carbonic oxide. Consequently, even if we assume that normal blood contains .15 per cent. of carbonic oxide, this is not more than would correspond to the experimental limit of error in Haldane and Smith's experiments, and its effects on the result would not be appreciable.

It should also be borne in mind that, as Gamgee has indicated, hæmoglobin exists in the corpuscles joined to a constituent (not yet differentiated), and that its saturation with carbonic oxide may not be as definite, or as simple, as it has been assumed in connection with the investigations of Haldane and Smith. It should, however, on the other hand, be mentioned that Hüfner (5), by means of the spectro-photometer obtained nearly the same results as to the percentage saturation of hæmoglobin with carbonic oxide as they did.

But perhaps the most serious objection which has been raised is that carbonic oxide is during these experiments oxidized in the blood by the oxy-hæmoglobin, as St Martin suggests, or more likely in the tissues, especially as oxidation is known to take place in them more readily than outside the body; and this action might go on more freely when carbonic oxide is breathed, as it no doubt renders the metabolism somewhat abnormal. To solve this difficult problem, several investigations have been conducted by different physiologists, but the results obtained are very discordant. Gaglio (6) kept rabbits and pigeons under examination for ten hours, and observed no diminution in the amount of carbonic oxide from oxidation. St Martin arrived at nearly the same conclusion as Gaglio, although he thought there was a slight amount of oxidation. Haldane and Smith (7) in their experiments on men whose blood was 30 per cent. saturated with carbonic oxide, were unable to detect any difference in the saturation after the lapse of an hour, when the carbonic oxide was not allowed to escape by the lungs. On the other hand, Wachholtz (8) recently placed insects, frogs, and mice in vessels containing a mixture of oxygen and carbonic oxide, and after twenty-four hours he found that with mice particularly, the carbonic oxide had in several cases completely disappeared from the mixture. The frogs, though their blood showed carbonic oxide hæmoglobin with the spectro-scope, gave off little or no carbonic oxide to the receiver of a

gas pump. In a control experiment, where a corresponding mixture of oxygen and carbonic oxide was placed in a vessel, no diminution in the amount of carbonic oxide occurred. Wachholtz infers that the greater part of the carbonic oxide inspired is oxidized in the tissues and converted into carbon dioxide.

Dr Haldane, in a letter, informs me that he has recently repeated Wachholtz's experiments on mice, using the same percentage of carbonic oxide, and the same size of vessel and number of mice, but purposely allowing the animals to breathe air in place of oxygen. He says: "The result was that instead of the whole of the carbonic oxide disappearing within twenty-four hours, as in Wachholtz's experiments, there was not the very slightest disappearance of carbonic oxide even after thirty hours. Care was taken to render impossible any leakage of carbonic oxide outwards, and the analyses were made by a rigorously accurate method. The animals continued to show symptoms of carbonic oxide poisoning from the beginning to the termination of the experiment, and the blood of one killed at the end was 67 per cent. saturated with carbonic oxide, which is just what would have been expected from the percentage of carbonic oxide present in the air. The other animals recovered within a few minutes on being taken out. The experiments thus completely confirmed those of Gaglio." Having regard to the great experience of Haldane in the conduct of experiments of this kind, I incline to his conclusions, and hold that the weight of evidence is against the oxidation of carbonic oxide in the body.

We may now take into consideration the marked discrepancy between the oxygen tensions as made out by the carbonic oxide method, and those by the aërotonometer, or those inferred, according to Hüfner's data, from the determinations with the gas pump by Pflüger and others. In explanation of the difference, Haldane and Smith have put forward a number of important facts, only some of which I shall mention. They say that oxygen is admittedly absorbed by the red, and possibly by the white corpuscles of the blood during its flow from the artery to the gas pump, this in one case of Pflüger's being as much as 10 per cent. when the experiment was slowly performed, so that the results by the pump are too low, whereas no such



absorption of carbonic oxide takes place when it is breathed; and that in asphyxia the blood yields little or no oxygen to the gas pump, though on spectroscopic examination of the blood in the jugular vein the bands of oxyhæmoglobin are visible. To these I may add that in Fredericq's experiments the animals were, according to Lorrain Smith's recent investigations, in an abnormal state with regard to their respiration, from loss of blood and from having been kept for some time in an uncomfortable position, etc., as well as from their blood having been peptonized.

After full consideration of the evidence on both sides, unprejudiced observers will, I think, admit that we cannot accept as conclusive the results obtained by either method. The great variations in the oxygen tensions, as made out by Haldane and Smith, at different times, in man (16 per cent., 26 per cent., and 38 per cent.), indicate that there is some foundation for this criticism. Besides, some physiologists, regarding the aërotonometer method as the more direct and the more reliable one for taking the tension of gases, are not prepared at present to put aside the results obtained by it; but certainly from what I have said, it is evident that investigations with the gas pump should be repeated, in order to avoid, as far as possible, the fallacy to which I have already alluded.

II. We may now consider the importance of the second factor—the chemical affinity of the hæmoglobin of the blood.

Some years ago, E. J. Mills (9), by causing barium sulphate to be formed between two parallel glass plates placed nearly in contact, tried to prove that "chemical change can take place at a distance." If his opinion were correct, there would be no difficulty in understanding how the affinity of the hæmoglobin in the red blood-corpuscles might exercise itself on the oxygen of the air of the alveoli across the thin layer of plasma and the film formed by the endothelial lining of the alveoli and of the capillary wall together. Chemists, however, do not regard the evidence in favour of Mills's view as sufficient. But, undoubtedly, the hæmoglobin in the red corpuscles, by constantly absorbing oxygen from the plasma around them, lowers its oxygen tension, as Foster has pointed out, and thus indirectly causes more oxygen to enter the blood from the air-cells by diffusion.

An experiment devised by Max Verworn (10) may be modified and used to exemplify how diffusion or osmosis is influenced by chemical affinity. Thus, we may place in the outer vessel of a dialyser (fig. 1) a diffusible salt solution as of chloride of sodium, and in the inner vessel a solution of a substance such as gelatin, which does not diffuse through the membrane but exerts a chemical affinity, or rather "elective" action (11) for the salt in the vessel outside.<sup>1</sup> As the salt diffuses into the inner vessel,

FIG. 1.—a. Solution of gelatin. b. Solution of common salt.  
From *British Medical Journal*, 1899.

it forms there with the substance a combination (not a true chemical compound), and if it be assumed that this combination or "loose" compound is being continually carried off and replaced by a fresh salt solution, we shall find that the salt will soon have left the outer vessel. Now the hæmoglobin in the red corpuscles in the capillaries of the lung (fig. 2) would represent the indiffusible substance in the inner vessel of the dialyser, and the oxygen in the plasma (or in the alveoli) would correspond with the salt in the outer vessel; but of course the cases are

<sup>1</sup> Hofmeister has pointed out that gelatin (at least in the form of jelly) takes up methyl violet from water by what Ostwald terms "mechanical affinity" (12). The above experiment might accordingly be varied so that the outer vessel should contain methyl-violet instead of sodium chloride.

not exactly parallel, for in the lungs chemical affinity acts in all probability more as an adjunct to diffusion than as an agent by itself.

III. The third factor said to be concerned in the entrance of oxygen into the blood is the action of the endothelial cells of the alveoli and of the blood-capillary walls in *secreting* the oxygen from the air in the air-cells into the blood.

In its favour we have the fact that in the secretion of urine, and possibly in the transudation of lymph, the endothelium containing living protoplasm, discharges a somewhat analogous function. Again, there are some grounds for believing that epithelial cells may be the active agents in causing the passage of oxygen from the maternal to the foetal blood in the placenta, as its tension is only slightly greater in the former than in the latter.



FIG. 2.— $\alpha$   $\alpha'$ . Endothelial cells of alveolar wall and capillary wall together form a moist film.

Besides, Regnard and Schloesig have (13) ascertained that the amount of nitrogen and argon in the blood of the horse is approximately double what it ought to be if only solution took place, and they suggest that the alveolar membrane takes an active part in causing the solution of abnormal quantities of the gases. And when animals respire pure hydrogen or nitrogen, no oxygen, as Pflüger has pointed out (14), passes from the blood to the air in the alveoli.

Moreover, the remarkable changes in the oxygen tension of the arterial blood during great diminution of the oxygen tension of the air breathed, and in pathological states of the lungs—in fevers, etc., as discovered by Haldane and Smith (15)—cannot be accounted for by diffusion, even when aided by the chemical affinity of the hæmoglobin.

But the most direct and convincing evidence in support of this view we find in the case of the swimming bladder of fishes (16), in which oxygen, nitrogen, and possibly argon are secreted like saliva under the influence of the nervous system, whilst the fresh wall of the bladder will scarcely allow oxygen to pass even under the pressure of one atmosphere.

Finally, though we are not yet in a position to pronounce dogmatically upon the subject of this paper, I am convinced that the entrance of oxygen into the blood in the lungs depends first, on diffusion, supplemented and modified largely by the indirect agency of the chemical affinity of the hæmoglobin in the corpuscles; and secondly, in all probability, on the secretory activity of the endothelial wall of the alveoli and of the capillary walls, and this activity may be supposed to act against or along with diffusion. But the view which attributes the entrance of oxygen to diffusion, even with the aid of chemical affinity, must, I think, be regarded as improbable.

I desire, in conclusion, to express my sincere obligations to Dr Haldane and to Dr Lorrain Smith for information which they have so kindly communicated to me with respect to the details of their experiments and their views.

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#### APPENDIX.

|  |   |   |
|--|---|---|
| <i>Tension of oxygen in the dog, in percentages of an atmosphere (17), .</i> | { | In external air, 20·95 per cent. (= 159 mm. Hg.)                                      |
|  |   | In alveolar air, 18 per cent. (Loewy 13=99 mm. Hg., but others say 114 mm. Hg.)       |
|  |   | In arterial blood, 14 per cent. (Haldane and Smith 26·2 per cent., or 38·5 per cent.) |
|  |   | In the tissues, 0.  |

The percentage of oxygen in the gases in the swimming bladder of fishes may be as high as 85 per cent., though the tension of oxygen in the water around them cannot be greater than 21 per cent. of an atmosphere (18).

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- (6) *Archiv. f. Exp. Pathologie*, 1887, Band 22, p. 233.
- (7) *Journal of Physiology*, 1896, p. 515.
- (8) *Pflüger's Archiv*, February 1899, p. 174.
- (9) *Journal of Chemical Society*, 1880, p. 693.
- (10) *General Physiology*, translated by Lee, p. 527.
- (11) *Schäfer's Text-Book of Physiology*, p. 276.
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- (14) *Howell's Text-Book of Physiology*, p. 526.
- (15) *Journal of Physiology*, 1897, p. 244; and 1898, p. 307; and 1899, p. 19.
- (16) *Schäfer's Text-Book of Physiology*, p. 705; and *Stewart's Manual of Physiology*, 1899, p. 243.
- (17) This table is constructed partly from *Schäfer's Text-Book of Physiology*, p. 778.
- (18) *Schäfer's Text-Book of Physiology*, p. 705.
- (19) *Journal of Physiology*, 1899; 25, p. 33.

I may add that Vaughan Harley (19) has recently found that after compression of one lung in dogs, more oxygen is absorbed and more carbon dioxide is eliminated. He is unable to explain the result except by supposing, with Bohr, that carbon dioxide is secreted by the epithelium of the air-cells.

THE TOPOGRAPHY OF THE FACIAL NERVE IN ITS  
RELATION TO MASTOID OPERATIONS.<sup>1</sup> By ROBERT  
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IN two papers on the applied anatomy of the mastoid region, published in the *Transactions* of the Royal Academy of Medicine, Ireland, 1890-1891, Professor Birmingham recorded the examination of 100 temporal bones, in which he had investigated the chief relations of the mastoid antrum and the anatomy of the operations for opening that cavity. In these papers the relations of the facial nerve were but briefly referred to, and at Dr Birmingham's suggestion I have carried out in his laboratory a systematic examination of thirty temporal bones, with the object of determining the precise relations of this nerve to the exterior of the skull in the adult, its depth, as well as that of the external semicircular canal, from the surface, and the relations of both these structures to the operations for exposing the mastoid antrum and to 'the radical operation.'

For the material upon which the investigation was carried out, and for many valuable suggestions, I am greatly indebted to Professor Birmingham.

METHOD.

Each bone was cut from before backwards, beginning near the angle between the squamous and petrous portion, so as to expose the aqueduct of Fallopius in its entire length; the external semicircular canal was also cut across by the same section in every case (see figs. 1 and 2).

Then I projected the facial canal on the surface by a method devised by Professor Birmingham in his investigations, namely,

<sup>1</sup> Read before the Sixth International Otological Congress, London, August 1899.

the method of drilling from the exposed canal transversely outwards. In order to utilise this method, it was necessary to make the holes accurately at right angles to the sagittal plane, and of course thus parallel to one another. To do this I constructed the following simple contrivance.

An accurately made wheel-drill was fastened down on a sliding bed, so that the drill was capable of backward and forward movement only, without any lateral wobbling. To the end of the base-board, in which the sliding drill-bed moved, I fastened an end-board at right angles to the line in which the drill worked, in such a way that it could be shifted about in a vertical plane perpendicular to the line of the drill. Each temporal bone was now accurately fastened in correct position to this end-board, with the exposed facial canal towards the drill, by

FIG. 1.—Temporal bone (left) on edge, and looked at from above, showing position of cut.

embedding it in dentists' 'modelling composition.' This material, which becomes soft in hot water and hard again in cold, is very suitable for such a purpose. Thus, the drill always working in the same direction, and the bone capable of adjustment, while remaining in the plane at right angles to the drill (*i.e.*, sagittal, as the bone was in correct position), I was enabled to get on the outer surface a perfectly true projection of the facial canal.

Next I measured, with the aid of a fine sliding callipers, graduated to  $\frac{1}{2}$  millimetres, the distance of the facial canal from three points on the surface (fig. 4)—*viz.*, *a*—a point immediately behind the external auditory meatus on a horizontal line

passing through its centre; *b*—a point immediately behind the upper part of the meatus, and immediately below a horizontal line passing through its upper margin; *c*—a point high up

FIG. 2.—Inner surface of right temporal bone, showing cut surface and facial and external semicircular canals.

above the middle of the meatus on the posterior roof of the zygoma.

The measurements from *a* and *b* were taken horizontally inwards and parallel to the posterior wall of the meatus; that

FIG. 3.—Drill fastened on its sliding bed; temporal bone in position ready for drilling.

from *c* straight in and slightly downwards to the horizontal part of the facial canal, which lies on the inner wall of the attic. I have not used the suprameatal spine in any of my measurements—first, because it is very frequently absent; and



secondly, because when it is present it varies considerably in length and shape. The points *a* and *b* are taken as representing the anterior edge or lip of the cavity made in the bone by the drill or chisel when the mastoid is opened below or above respectively. Also, the point *b* is the point from which, as Birmingham has shown, the antrum may in every case be tapped, without any danger to either the lateral sinus or the cranial cavity, by a small drill sent straight in, *i.e.*, perpendicular to the sagittal plane. The distance of the facial canal from the point

FIG. 4.—Outer surface of left temporal bone, showing points A, B, and C; and also position of line of projection of facial nerve.

*c* will come into consideration in removing the outer wall of the attic from the external meatus.

#### RESULTS.

The line of projection of the facial canal on the surface is very constant in position. It lies on the posterior and superior walls of the external auditory meatus, about midway between the sulcus tympanicus and the outer margin of the bony meatus, its position between these two points varying, however, with the obliquity of the meatus. The lower part of the canal is perpendicular or has a slight inclination forwards, and its upper part beyond the bend runs almost horizontally forwards, with a slight inclination upwards. As Politzer shows in his *Lehrbuch der Ohrenheilkunde*, in its whole course from above downwards the facial canal slopes out, being thus farther from the surface

above than from the surface below. In a transverse section inclining backwards and exposing the canal, it will be seen, however, that its inclination outwards is not regular and gradual when traced from above downwards, but that at the genu it frequently makes a bend either outwards or inwards, both directions being about equally common. As regards its relations to the surface of the mastoid, a straight drill hole, 3 to 4 mm. behind the posterior wall of the meatus and parallel to that wall, will in every case strike it. This last holds true from the level of the floor of the meatus to within 4 mm. of the roof.

I have found the distance of the facial canal from the surface to vary very considerably. From the first point *a*, immediately behind the meatus, and on a horizontal line passing through its centre, its average distance was about 16·75 mm., the maximum being 22 mm. and the minimum 13·25 mm. In the case where it measured 22 mm., the surface of the mastoid at the measuring point was considerably bulged out.

*Distance of Facial Canal from point a.*

|                      |                     |
|----------------------|---------------------|
| 1 case was 22 mm.    | 5 cases were 17 mm. |
| 2 cases were 19·5 "  | 5 " " 16 "          |
| 2 " " 18·75 "        | 2 " " 15·25 "       |
| 4 " " 18 "           | 2 " " 14·5 "        |
| 1 case was 17·75 "   | 3 " " 14 "          |
| 2 cases were 17·25 " | 1 case was 13·25 "  |

From the second point *b*, immediately behind the upper part of the meatus and immediately below a horizontal line passing through its upper margin, the average distance was about 18·5 mm., the maximum being 22·75 mm. and the minimum 14·75 mm., this last being a case of solid mastoid. The first (22·75 mm.) was in the same case as gave the maximum distance from the point *a*.

*Distance of the Facial Canal from point b.*

|                      |                        |
|----------------------|------------------------|
| 1 case was 22·75 mm. | 2 cases were 17·75 mm. |
| 4 cases were 21·25 " | 1 case was 16·75 "     |
| 1 case was 20·5 "    | 2 cases were 16 "      |
| 3 cases were 20 "    | 1 case was 15·75 "     |
| 2 " " 19·25 "        | 3 cases were 15 "      |
| 4 " " 19 "           | 1 case was 14·75 "     |
| 5 " " 18·5 "         |                        |

From the third point *c*, above the middle of the meatus on the posterior root of the zygoma, the average distance was about 19.4 mm., the maximum being 21.75 mm. and the minimum 17 mm.

*Distance of Facial Nerve from point c.*

|              |           |              |          |
|--------------|-----------|--------------|----------|
| 1 case was   | 21.75 mm. | 4 cases were | 18.5 mm. |
| 2 cases were | 21.25 "   | 2 " "        | 18 "     |
| 2 " "        | 21 "      | 1 case was   | 17.75 "  |
| 4 " "        | 20.75 "   | 2 cases were | 17.25 "  |
| 6 " "        | 20 "      | 1 case was   | 17 "     |
| 5 " "        | 19 "      |              |          |

As mentioned above, the external semicircular canal was always exposed by the same cut as opened up the facial canal. Its outer sweep lies about 1.5 mm. above the horizontal part of the facial canal and parallel to it. Its depth from the surface was measured from the points *b* and *c*.

From *b* the average distance was about 18.56 mm., the maximum being 22 mm. and the minimum 13.75 (this last in a solid mastoid).

*Distance of the External Semicircular Canal from point b.*

|              |         |              |           |
|--------------|---------|--------------|-----------|
| 1 case was   | 22 mm.  | 1 case was   | 17.75 mm. |
| 1 " "        | 21.25 " | 5 cases were | 17.5 "    |
| 3 cases were | 20.75 " | 2 " "        | 15.5 "    |
| 4 " "        | 20 "    | 2 " "        | 14.75 "   |
| 2 " "        | 19.75 " | 2 " "        | 14.5 "    |
| 4 " "        | 19.25 " | 1 case was   | 13.75 "   |
| 2 " "        | 18.5 "  |              |           |

From the point *c* the average distance was about 18.5 mm., the maximum being 20.5 mm. and the minimum 16.25 mm.

*Distance of the External Semicircular Canal from point c.*

|              |          |              |           |
|--------------|----------|--------------|-----------|
| 1 case was   | 20.5 mm. | 3 cases were | 18.25 mm. |
| 1 " "        | 20.25 "  | 5 " "        | 18 "      |
| 5 cases were | 20 "     | 5 " "        | 17.25 "   |
| 3 " "        | 19.5 "   | 2 " "        | 17 "      |
| 4 " "        | 19 "     | 1 case was   | 16.25 "   |

## SUMMARY.

1. The facial canal lies altogether in front of the anterior border of the mastoid process, and a drill sent *straight in* from the surface of the mastoid (point *b*) to open the antrum, cannot injure the nerve.

2. Measured from the point *b*, and along a line sloping slightly more forwards than the posterior wall of the meatus, and also slightly upwards, the facial canal, in 43·3 per cent. of cases, was more superficial than the external semicircular canal; in the same percentage of cases this was just reversed, and in the remaining 13·4 per cent. they were the same distance from the surface (at *b*). Thus the external semicircular canal cannot be taken as a guide to the depth of the facial nerve. The distance between the facial and the semicircular canals, measured in the same way (*i.e.*, from the point *b* slightly upwards, and in a direction more forwards than the posterior wall of the meatus), was never more than 1·5 mm., except in one case where the latter was 4·25 mm. more superficial than the former.

3. The average distance of the facial canal from the point *b* is slightly *less* than that of the semicircular canal when the measurements are made to corresponding points on both (*i.e.*, points on the same perpendicular line).

4. In order to avoid the facial canal in every case while drilling the mastoid from the point *a*, the drill-hole must never be more than 13 mm. deep if it is horizontal and parallel to the posterior wall of the meatus.

5. From the point *b*, 14·5 mm. must be the maximum depth of the hole, if it is horizontal and parallel to the posterior wall of the meatus; but if the drill or chisel be sent in with a stronger inclination forwards, and also slightly upwards, the greatest safe depth would be 13·5 mm., as in one of the specimens the external semicircular canal was only 13·75 mm. from this point.

6. The anterior lip of the bone wound, as above, is the point from which these measurements are to be taken.

7. It has been stated that the points *a* and *b* are immediately behind the meatus; but on account of the gradual way in which the surface of the mastoid slopes into the meatus, and

as the drill has to be kept parallel to the posterior wall of the meatus, it is not possible to make a drill-hole nearer to this posterior wall than about 3 mm. In other words, a line drawn inwards from either *a* or *b* parallel to the posterior wall of the meatus will be about 3 mm. distant from the meatus—the measurement being taken, of course, at a point in the canal sufficiently far in to be beyond the gradual slope leading from the mastoid into the meatus.

8. In removing the outer wall of the attic, it should be remembered that the external semicircular canal is almost always (91 per cent.) nearer the surface of the skull at the point *c* than the facial nerve; but as it is about 1.5 mm. higher than the latter, it is almost out of danger; besides, it has a thicker covering of compact bone in this situation than the facial nerve. From the meatus the chisel or scoop ought not to go in more than 16.5 mm., or, if sent in very high, 16 mm., measured from the point *c*.

CRANIOMETRIC OBSERVATIONS IN THE POST-MORTEM ROOM. By DAVID WATERSTON, M.B., F.R.C.S.E., *Demonstrator of Anatomy, Edinburgh University.*

OUR knowledge of the shapes and dimensions of skulls has been obtained chiefly from measurements of dried and macerated specimens, and partly from measurements of the head in the living subject. The latter method, however, is not entirely accurate, since it involves the use of external surface-marks for the deeper bony points, and includes the thickness of the soft tissues, both of which create some inaccuracies in the results. No use has hitherto been made, as far as I am aware, of the opportunities afforded by post-mortem examinations for the collection of craniometric information. But any accurate measurements obtained from this source would be of great value, since, at the same time, information could be obtained regarding the character of the brain of the same subject. Combined information of this kind is essential for an investigation into the relationship between the size and shape of the skull and the associated pattern of cerebral convolutions, and into such subjects as the craniology of the skulls of the insane, since macerated skulls of such a kind are practically unobtainable, in this country at least.

The practical difficulties have hitherto prevented such information being obtained, but these difficulties do not form an insuperable obstacle; and, at the suggestion of Dr Ford Robertson, of the Scottish Asylums Laboratory, I have devised a method by which the necessary measurements can be obtained at an ordinary post-mortem examination without much trouble, and without any additional disfigurement of the head, and this method will, I trust, be of use to anatomists and pathologists. The difficulties to be overcome are met with, first, in exposing the essential bony points; and, second, in measuring the intervening distances.

(1) The bony points on the vault are easily accessible, as it

is only necessary to make the usual transverse incision across the head, from ear to ear, and to reflect the flaps forwards and backwards a little further than usual, so as to expose the nasion in front and the occipital point behind. The temporal muscle should also be reflected from its fossa on either side.

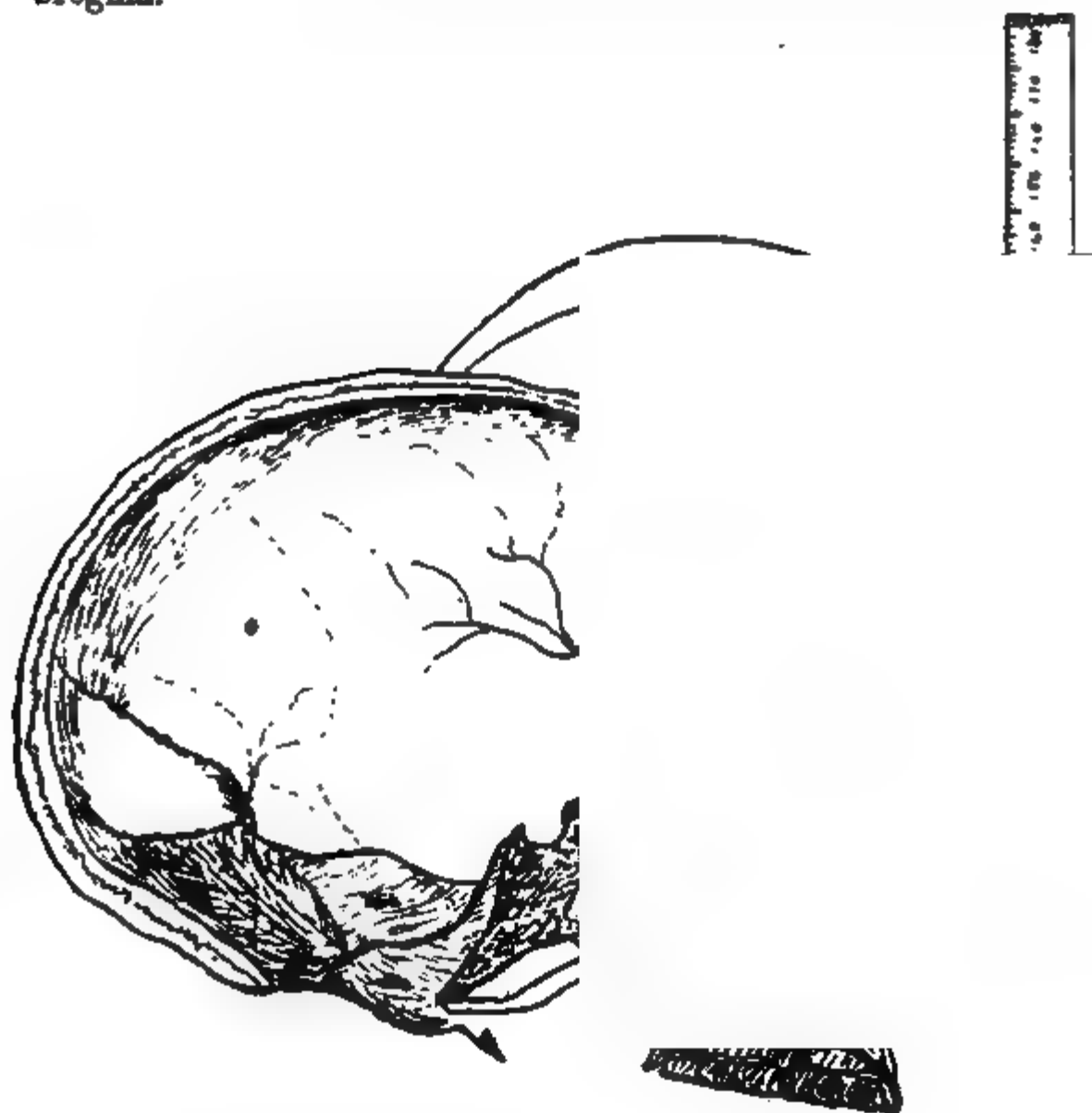
But a little dissection is necessary to expose the point on the base of the skull from which measurements of the height and of the prognathism of the skull require to be taken, and the ordinary calipers are of a shape unsuitable for taking the measurements.

The basion is best reached from the anterior aspect, where it is only separated from the pharyngeal cavity by the mucous membrane and some ligamentous bands. The mouth should be opened to its full extent, and the posterior wall of the pharynx examined with the forefinger, and the bony prominences there carefully identified. At the level of the hard palate a prominent bony transverse ridge is readily felt: this is the anterior arch of the atlas vertebra, and on its centre is a well-marked tubercle. About half-an-inch above this the pharyngeal tubercle of the basi-occipital bone is felt, and between these two points lies the basion. A sharp-pointed knife is now to be passed along the forefinger, and a transverse incision about an inch and a-half in length made between the bony points, dividing the mucous membrane, the anterior ligament between the atlas and the occiput, and the fibres passing from the odontoid process to the same region. In fact, the under surface of the anterior margin of the foramen magnum is cleared, and, practically, this is found to be a very easy matter, when the bony points have been made out. As a preliminary, it is advisable to swab out the mouth with a small sponge moistened with spirit, and a rubber glove is useful in protecting the hand from any sharp edges of the teeth, without seriously affecting the tactile sense.

(2) In taking the measurements, a suitable kind of caliper must be used; and the form of instrument devised and described by Dr Hepburn<sup>1</sup> is very good, as, by it, measurements of asymmetry can be taken.

<sup>1</sup> Hepburn, *Proc. Royal Soc. of Edin.*, vol. xxii., 1899.

An additional limb must, however, be used to take the measurements from the basion, in place of one of the curved limbs of this instrument. This limb must be shaped so that its free end can be brought against the basion from the mouth or nose, while at the same time the rest of the instrument is free to move, so that the other limb can be made to touch the bregma.



Form of limb, and method of using, in unskinned skull.

The illustration shows the shape of a limb suitable for this purpose, and the way in which it is intended to be used. The limb springs from the centre of the socket which fixes it to the caliper-bar. The convex side of the limb faces the opposite limb.

The terminal straight part, or beak, is the part applied to the basion, and the upper edge of this part is in line with the lower



edge of the socket, and this lower edge is fixed at zero on the caliper.

It will be found to be very easy to pass this limb along the floor of the nose to the pharynx, and, with the forefinger in the mouth, to guide the beak into the incision on the pharyngeal wall, and to fix it against the exposed margin of the foramen magnum. The beak also prevents the point from being passed too far in.

The shape of the limb allows the other limb to be brought to the bregma without interference from the floor of the nose; but if the bregma be unusually far forward, the lower limb may be introduced from the mouth, which overcomes the difficulty.

The head of the subject should be allowed to hang over the end of the table, so as to increase the distance between the basion and the atlas, and the point of the limb be kept carefully against the floor of the nose while being introduced.

The basi-alveolar length is measured by inserting a straight rod into the mouth, and fixing its extremity against the basion, and then measuring the distance from this point to a point between the upper central incisor teeth on the alveolar margin.

The basi-nasal length should be taken after removal of the skull-cap and brain, by measuring from above, using the special limb described to fix against the anterior margin of the foramen magnum from the inner side, while the other bar is brought against the nasion, after removing the skull-cap, and taking out the brain.

Finally, the capacity of the skull is to be estimated, by filling the skull-cap and the base of the skull with water (after plugging the apertures with putty), and measuring the amount of the fluid contained in each (according to the method of Zanke).<sup>1</sup>

Dr Robertson and I have, in this way, succeeded in taking the measurements of several skulls in the post-mortem and in the dissecting-rooms, and have tested its accuracy by comparing the results of independent observations on the same skull. After a slight amount of practice, we found that the figures obtained were practically identical; and this has led us to believe that the method is capable of yielding accurate and satisfactory results, which should be of special interest when combined with information regarding the brain contained within this measured skull.

<sup>1</sup> Zanke, *Neurologisches Centralblatt*, No. 11, June 1897.

**NINTH REPORT OF THE COMMITTEE OF COLLECTIVE  
INVESTIGATION OF THE ANATOMICAL SOCIETY  
OF GREAT BRITAIN AND IRELAND FOR THE  
YEAR 1898-99. Reported by F. G. PARSONS.**

IN October 1898 the following subject for Collective Investigation was sent to the various anatomical schools in the United Kingdom :—

“The positions at which the Internal Circumflex, External Circumflex, and Perforating Arteries of the Thigh arise.”

Returns were received from the following gentlemen :—

D. Waterston, M.B., Edinburgh University ; Alex. Low, M.B., Aberdeen University ; H. H. Broome, M.B., Owens College, Manchester ; W. H. Wynn, B.Sc., Mason College, Birmingham ; L. Phillips, M.B., St Bartholomew's Hospital ; N. Carpmael, St Thomas's Hospital ; Messrs Stusser and Ham, London Hospital.<sup>1</sup>

In compiling this Report the Editor has been careful not to include any material in which the measurements were not definite and which was not accompanied by clear and satisfactory diagrams. It seemed better to run the risk of excluding a large quantity of valuable statistics than to render the Report useless or misleading by admitting loose and inaccurate returns. The great disadvantage of a Collective Report is that the Editor is not, and cannot be expected to be responsible for the accuracy of the data on which he works ; hence he is either obliged to incorporate everything which is sent in, or to use his own judgment in rejecting material which appears to him inaccurate. In this Report the Editor feels fairly sure that the statistics used are reliable, and this feeling is borne out by the fact that, where the ground covered is the same, the averages tally fairly closely with those of previous recorders.

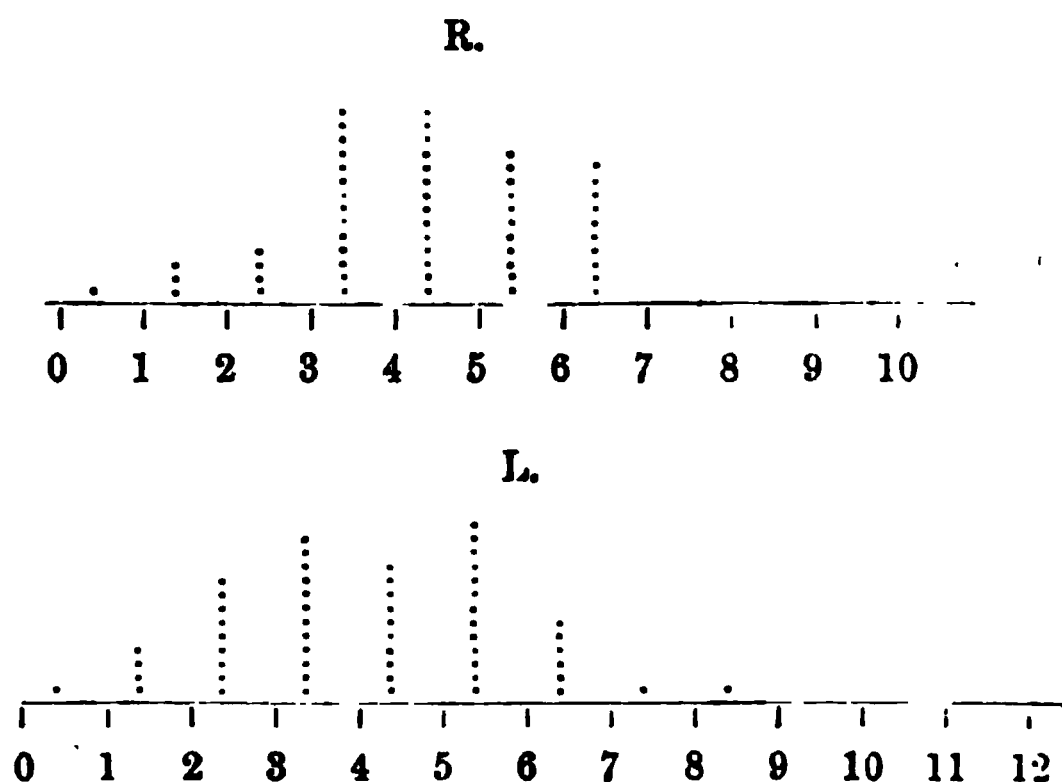
<sup>1</sup> A report was received from Dr C. J. Patten, of Trinity College, Dublin, but unfortunately it was too late to be incorporated.

## THE INTERNAL CIRCUMFLEX.

The internal circumflex was observed in 115 cases, 57 being on the right side and 58 on the left. The average of the distances between the origin of the artery and Poupart's ligament in all these cases was 4.2 cm., or rather less than  $1\frac{3}{4}$  inches.

It will be seen from the accompanying tables that the variation in origin is practically confined to a space some 5 cm. long, beginning about 2 cm. and ending about 7 cm. below Poupart's ligament. By a curious coincidence the average for the right and left sides worked out at the same figure, viz., 4.2 cm.

TABLE I.—*Distance of Origin of Internal Circumflex from Poupart's Ligament, in Centimetres.*



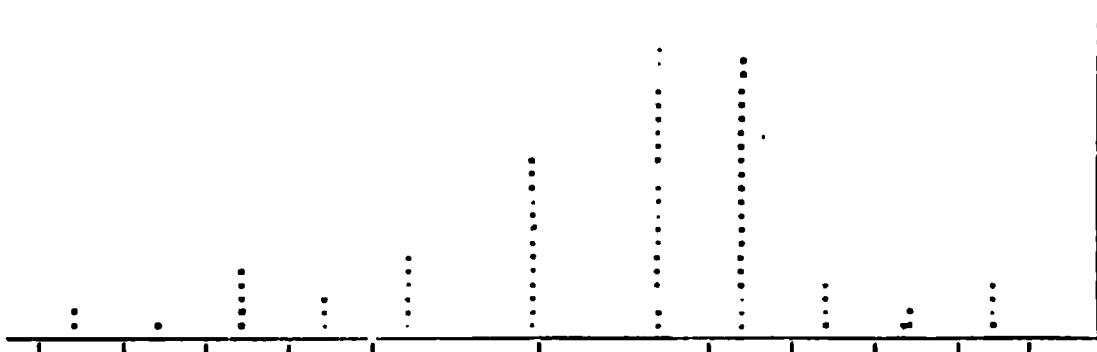
Although the artery usually rises from the inner side of the common or deep femoral, as the case may be, there is evidence that it may rise from any part of the circumference of the trunk, although this point was not paid sufficient attention to to enable us to draw up any definite statistics. In 1 case the artery rose from the front of the common femoral artery and arched over the front of the common femoral vein instead of passing behind it. In 2 cases, both on the left side, the internal circumflex rose from the deep epigastric artery (these have not been included in the previous or following tables). In 4 cases the artery was double, while in 1 case out of 66 on the right side (1.5 per cent.), and in 4 out of 60 on the left (6.6 per cent.) the internal and external circumflexes rose by a common trunk.

It has already been pointed out that the average point of origin of the internal circumflex in these observations is 4.2 cm. below Poupart's ligament. If we assume that the average point of division of the common femoral is  $1\frac{1}{2}$  inches, or 3.8 cm., below the same place, we should be led to the conclusion that the point of origin of the

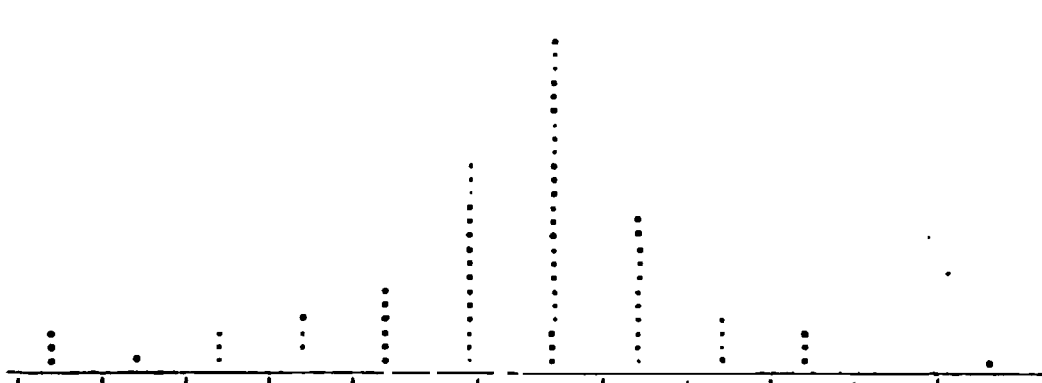
internal circumflex is from the deep femoral 0.4 cm., or less than quarter of an inch below the bifurcation of the common femoral. We have, fortunately, a considerable number of actual measurements of the distance between the internal circumflex and the bifurcation of the common femoral with which to check this conclusion.

TABLE II.—*Distance of the Origin of the Internal Circumflex Artery from the Bifurcation of the Common Femoral, in Centimetres.*

R.—Total number of Observations, 81.

|  |   |   |   |   |    |        |    |   |   |   |   |
|--|---|---|---|---|----|--------|----|---|---|---|---|
| 2  | 1 | 5 | 3 | 6 | 13 | 21     | 20 | 4 | 2 | 4 | Number of obser-<br>vations.                          |
|  |   |   |   |   |    |        |    |   |   |   |   |
| 5  | 4 | 3 | 2 | 1 | B. | 1      | 2  | 3 | 4 | 5 | Distance from bi-<br>furcation (B) in<br>centimetres. |
| Above.   |   |   |   |   |    | Below. |    |   |   |   |   |

L.—Total number of Observations, 75.

|  |   |   |   |   |    |        |    |   |   |   |   |
|--|---|---|---|---|----|--------|----|---|---|---|---|
| 3  | 1 | 3 | 4 | 6 | 15 | 24     | 11 | 4 | 3 | 1 | Number of obser-<br>vations.                          |
|  |   |   |   |   |    |        |    |   |   |   |   |
| 5  | 4 | 3 | 2 | 1 | B. | 1      | 2  | 3 | 4 | 5 | Distance from bifur-<br>cation (B) in<br>centimetres. |
| Above.   |   |   |   |   |    | Below. |    |   |   |   |   |

From the foregoing it will be obvious that in the greater number of cases the internal circumflex arose just below the point of bifurcation. Out of the 81 observations on the right side, the artery rose from the deep femoral in 51 (64 per cent.), from the common femoral in 17 (21 per cent.), and from the bifurcation in 13 (15 per cent.).

Out of the 75 observations on the left side the artery rose from the deep femoral in 43 (58 per cent.), from the common femoral in 17 (23 per cent.), and from the bifurcation in 15 (19 per cent.). These

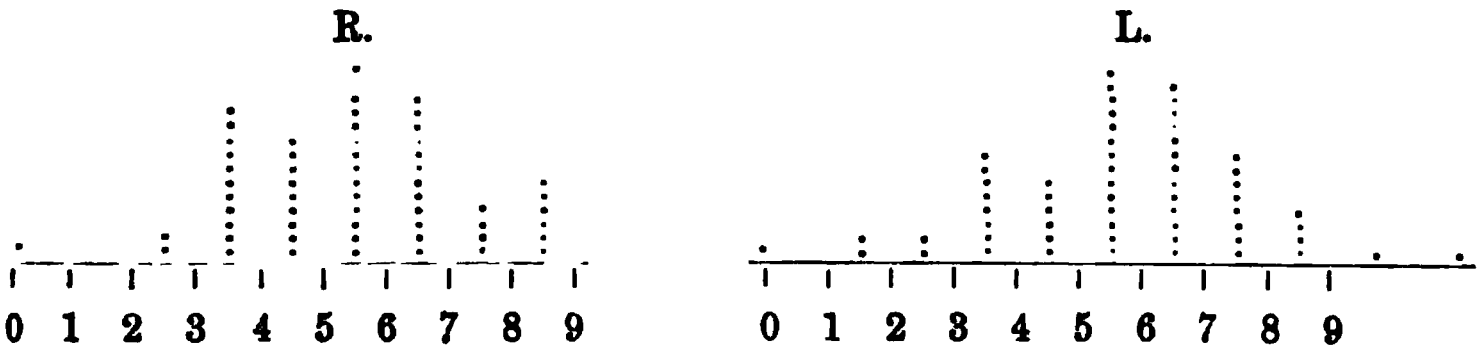
results closely agree with those recorded by Ruge,<sup>1</sup> when one allows for the separate group of arteries rising from the bifurcation.

THE EXTERNAL CIRCUMFLEX.

The distance between the origin of the external circumflex and Poupart's ligament was observed in 119 cases, 59 on the right side and 60 on the left. The average of the distances between the origin of the artery and Poupart's ligament in these 119 cases was 5.5 cm., or nearly 2¼ inches (5.4 cm. on the right and 5.7 cm. on the left).

The range of variation will be seen from the accompanying tables :—

TABLE III.—*Distance of Origin of External Circumflex from Poupart's Ligament, in Centimetres.*



From the foregoing it will be seen that the external circumflex, instead of rising opposite the internal, as is often stated, came off more than a centimetre lower down.

With regard to the simple question whether the external circumflex rises above or below the internal we have 162 records which we regard as trustworthy ; 84 of these are on the right side and 78 on the left. We propose to divide them into three divisions.

TABLE IV.—*Origin of the External Circumflex Artery with regard to that of the Internal Circumflex.*

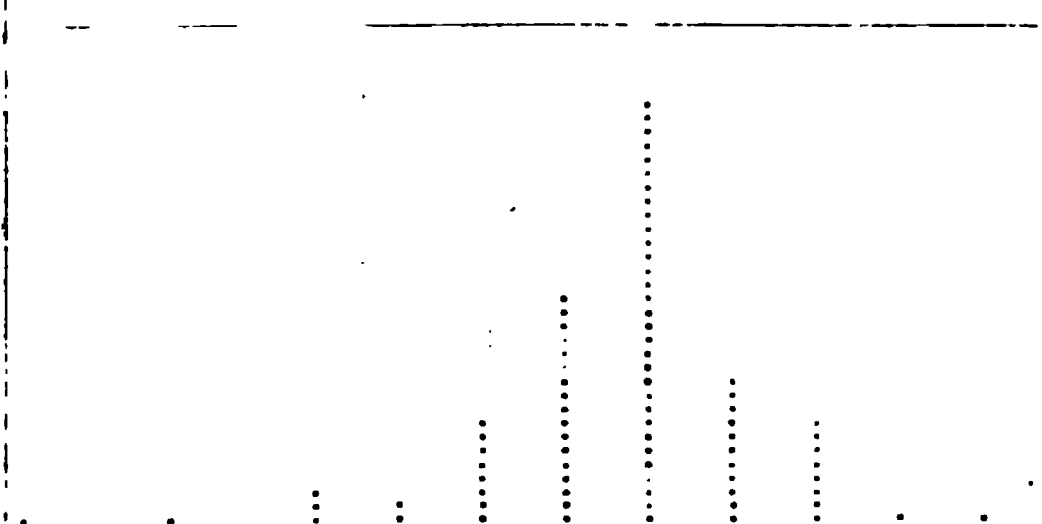
|   | R.       | L.       |
|---|----------|----------|
| A.—In which Ext. Circumflex rose above I. C.                      | 19 (23%) | 14 (18%) |
| B.—In which Ext. Circumflex rose opposite or in common with I. C. | 15 (18%) | 20 (26%) |
| C.—In which Ext. Circumflex rose below I. C.                      | 50 (59%) | 44 (56%) |
|   | 84       | 78       |

<sup>1</sup> "Varietaten im Gebeite der Arteria femoralis," *Morphol. Jahrbuch*, 1895, p. 217.

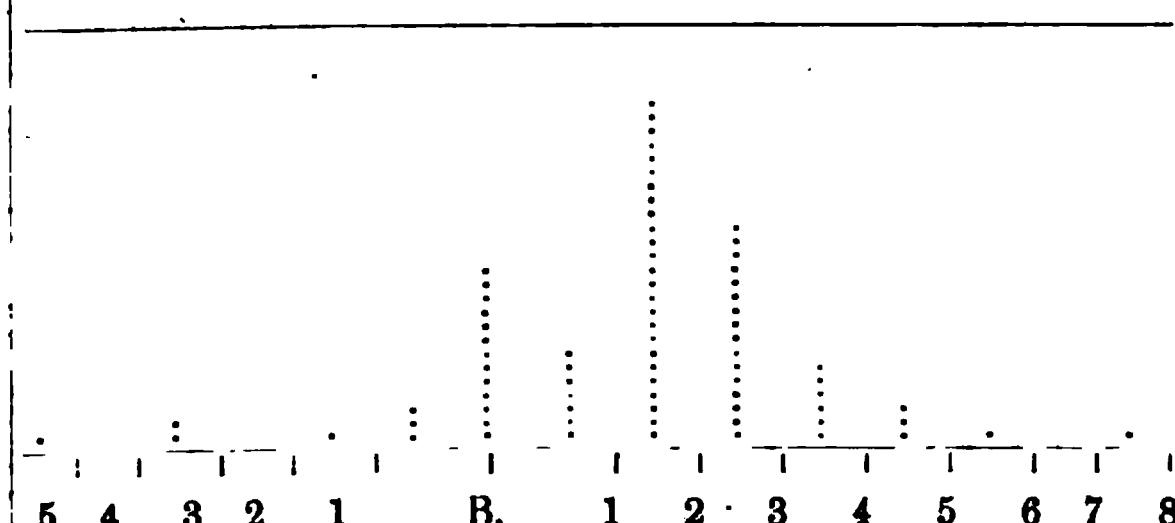
The next point to consider is the relation of the origin of the external circumflex to the point of bifurcation of the common femoral artery. On this point we have 163 observations, 84 on the right side and 79 on the left. The following tables show the variation which occurred in the material at our disposal.

TABLE V.—*Distance between the Origin of the External Circumflex Artery and the Bifurcation of the Common Femoral Artery.*

R.

|  |   |   |   |   |    |        |    |   |   |   |   |
|--|---|---|---|---|----|--------|----|---|---|---|---|
| 1  | 1 | 3 | 2 | 8 | 17 | 31     | 11 | 8 | 1 | 1 | Number of obser-<br>vations.                          |
|  |   |   |   |   |    |        |    |   |   |   |   |
| 5  | 4 | 3 | 2 | 1 | B. | 1      | 2  | 3 | 4 | 5 | Distance from bifur-<br>cation (B)<br>in centimetres. |
| Above.   |   |   |   |   |    | Below. |    |   |   |   |   |

L.

|  |   |   |   |    |    |        |    |   |   |   |   |                            |   |   |
|--|---|---|---|----|----|--------|----|---|---|---|---|----------------------------|---|---|
| 1  | 2 | 1 | 3 | 13 | 7  | 25     | 16 | 6 | 3 | 1 | 1 | Number of<br>observations. |   |   |
|  |   |   |   |    |    |        |    |   |   |   |   |                            |   |   |
| 5  | 4 | 3 | 2 | 1  | B. | 1      | 2  | 3 | 4 | 5 | 6 | 7                          | 8 | Distance from<br>bifurcation (B)<br>in centimetres. |
| Above.   |   |   |   |    |    | Below. |    |   |   |   |   |                            |   |   |

It is evident from these that the artery usually rises between 1 and 3 centimetres below the origin of the profunda. We have previously stated that the average of the distances of the origin of 119 external

circumflex arteries from Poupart's ligament was 5.5 cm., so that, if we assume that the bifurcation of the common femoral is  $1\frac{1}{2}$  inches, or 3.8 cm., below that ligament, the origin of the external circumflex would work out at 1.7 cm. below the bifurcation, a result which tallies very well with the arrangement shown in Table V.

It must not be supposed that all the cases recorded in Table V., in which the external circumflex rose below the bifurcation of the common femoral, were cases in which it necessarily rose from the deep femoral; as a matter of fact, in quite an appreciable number of cases it rose from the superficial femoral. To express this point clearly, it may be well to tabulate the 163 observations again in the following manner :—

TABLE VI.—*Arteries from which the External Circumflex Rose.*

|                                 | R.       | L.       |
|---------------------------------|----------|----------|
| Common femoral, . . . . .       | 7 (8%)   | 7 (9%)   |
| Point of bifurcation, . . . . . | 8 (9%)   | 13 (16%) |
| Deep femoral, . . . . .         | 64 (77%) | 56 (71%) |
| Superficial femoral, . . . . .  | 5 (6%)   | 3 (4%)   |
|                                 | 84       | 79       |

On comparing these with the similar statistics of the internal circumflex, it will be seen that the external circumflex, rose from the common femoral much less frequently than the internal circumflex did.

The number of cases in which the internal and external circumflexes rose by a common trunk has already been dealt with under the head of the internal circumflex.

The external circumflex occasionally rose by two trunks, and these cases have not been recorded among the 163 observations with which we have lately been dealing.

There were 3 cases of a double artery on the right side (3.5 per cent.) and 6 on the left (7 per cent.).

#### THE PERFORATING ARTERIES.

Unfortunately a large proportion of the observations of the origins of the perforating arteries were of no use to us, owing to the indefiniteness of the points from which measurements were taken. Many of the observers measured from the lower edge of the adductor brevis or pectineus, or other points which we have no means of fixing. In the Editor's opinion much of the responsibility for this rests with the Collective Investigation Committee, of which he was a member, in that it did not definitely state where it wished measurements to be

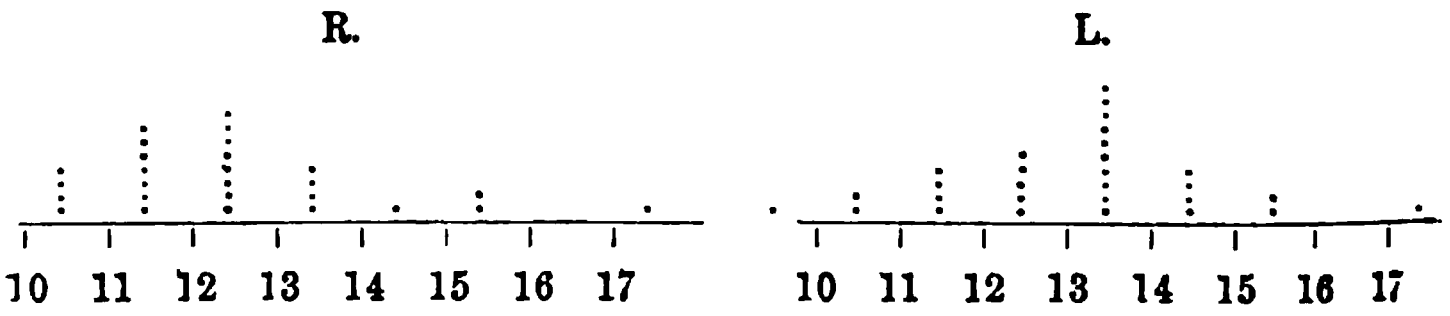
taken from. It is, however, best to record the observations which are definite, since, few though they are, they serve to give some idea of the place where the origins of the various arteries may be looked for.

There is some little difficulty in deciding on what should be described as a perforating artery. As the deep femoral runs down behind the adductor longus it gives off two sets of branches, an external set, which pass through small tendinous arches in the adductors quite close to their attachment to the femur, and an internal set, which often alternate with the first set, and disappear in the substance of the adductor magnus at some distance from the bone, and without having any fibrous aperture. As far as possible the first set only have been counted as perforating, but, unfortunately for attempts at strict classification, one or more of the external set are sometimes suppressed and their work done by the muscular branches of the internal set, which in these cases become really perforating arteries, their only characteristic being that they pierce the muscles at some little distance from the bone. Any attempt to rigidly confine the term perforating to the outer set only would lead to difficulties, since it sometimes happens that nearly all of the external set are absent or rudimentary, while their work is done by arteries which perforate the muscles at some little distance from the bone. The Editor has, therefore, been obliged to use his own judgment to some extent, and has included no material which was not accompanied by a clear diagram, as well as by apparently satisfactory and definite measurements.

FIRST PERFORATING ARTERY.

There are 56 observations of the distance of the origin of the first perforating artery from Poupart's ligament, 27 on the right side and 29 on the left. The average distance of the whole of these from Poupart's ligament works out at 13 cm., or about 5 inches. On the right side the average is 12·7 cm., on the left 13·3 cm. The range of variation will be seen from the accompanying tables:—

TABLE VII.—*Distance of Origin of First Perforating Artery from Poupart's Ligament, in Centimetres.*



The average distance of the origins of these 56 observations from the point of bifurcation of the common femoral, works out at



8 cm. ( $3\frac{1}{8}$  inches); 7.8 cm. on the right side, and 8.2 cm. on the left. The range of variation is as follows:—

TABLE VIII.—*Distance of the Origin of the First Perforating Artery from the Bifurcation of the Common Femoral, in Centimetres.*



In by far the greater number of cases the first perforating artery perforates the adductor magnus and adductor brevis, occasionally it perforates the pectineus also, very rarely it perforates the adductor magnus above the insertion of the adductor brevis. The number of cases may be tabulated in the following way:—

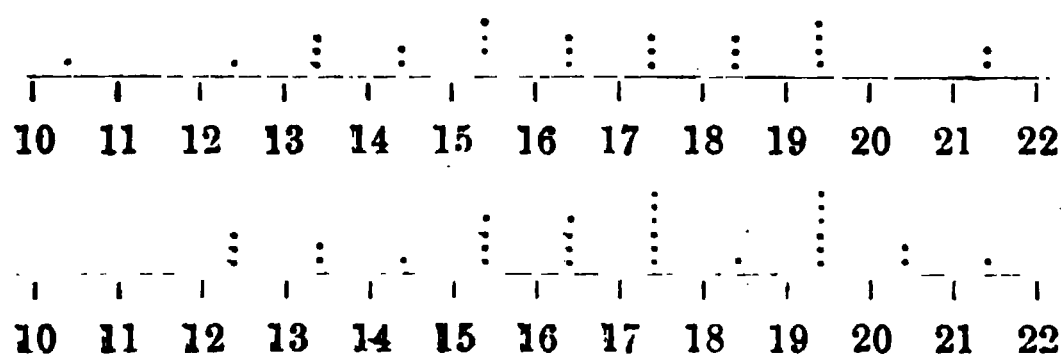
TABLE IX.—*Muscles which are perforated by the First Perforating Artery.*

|   | R.         | L.         |
|---|------------|------------|
| Adductors, brevis and magnus, . . . . .             | 32 (86.5%) | 35 (89.8%) |
| Adductors, brevis, magnus, and pectineus, . . . . . | 4 (10.8%)  | 2 (5.1%)   |
| Adductor magnus only, . . . . .                     | 1 (2.7%)   | 2 (5.1%)   |
|   | 37         | 39         |

## SECOND PERFORATING ARTERY.

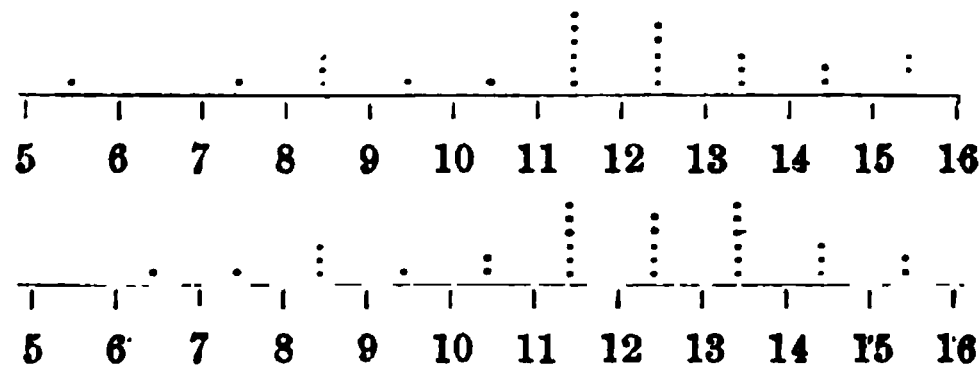
There are 56 observations of the distance of the origin of the second perforating artery from Poupart's ligament; 26 on the right side, and 30 on the left. The average distance of the whole of these from Poupart's ligament works out at 16.8 cm., or about  $6\frac{1}{4}$  inches. On the right side the average is 16.6 cm., and on the left 17.1. The following table shows the range of variation:—

TABLE X.—*Distance of Origin of Second Perforating Artery from Poupart's Ligament, in Centimetres.*



The average distance of the origin of the second perforating artery from the bifurcation of the common femoral in these 56 cases is 11·9 cm., or rather less than 5 inches. On the right side the average is 11·8 cm., and on the left 12 cm. The range of variation is shown in the following table:—

TABLE XI.—*Distance of Origin of Second Perforating Artery from Bifurcation of Common Femoral, in Centimetres.*



In the greater number of cases the artery pierces the adductor brevis and magnus, but occasionally it perforates the magnus below the insertion of the brevis.

TABLE XII.—*Muscles which are perforated by the Second Perforating Artery.*

|                               | R.         | L.         |
|-------------------------------|------------|------------|
| Adductors, magnus and brevis, | 20 (79·6%) | 19 (63·5%) |
| Adductor magnus only,         | 6 (20·4%)  | 11 (36·5%) |
|                               | 26         | 30         |

The second perforating artery occasionally rises by a common trunk with the first or third, or even with the first and third. The frequency of these arrangements in our cases was as follows:—

TABLE XIII.—*Mode of Origin of the Second Perforating Artery.*

|   | R.         | L.         |
|---|------------|------------|
| 1. By a single trunk,                                 | 18 (69·3%) | 23 (76·8%) |
| 2. By a common trunk with 1st perforating,            | 5 (19·2%)  | 2 (6·6%)   |
| 3. By a common trunk with 3rd perforating,            | 3 (11·5%)  | 4 (13·3%)  |
| 4. By a common trunk with the 1st and 3rd perforating | 0          | 1 (3·3%)   |
|   | 26         | 30         |

THIRD PERFORATING.

A third perforating branch from the profunda is not always present ; occasionally the second perforating may form the terminal branch ; but in these cases there are usually one or two perforating arteries from the superficial femoral. This happened once on the right side in 27 subjects, and once on the left in 29 ; it occurred on the two sides of one subject.

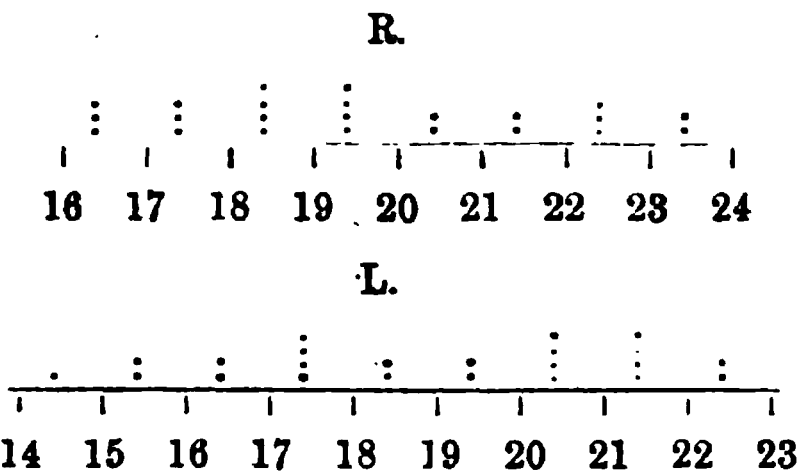
The third perforating is fairly often the terminal branch of the profunda, so that, if the terminal branch is included as a perforating, there may be two, three, four, or five of these.

In those cases in which the third perforating is the terminal branch of the profunda, it is useless to give the point at which it comes off, since that would be the point of origin of the second perforating. We shall therefore only consider the origin of the 46 cases (23 on each side) in which the third perforating is not the terminal branch.

The average distance of the origin of the artery from Poupart's ligament in these 46 cases is 19·5 cm., or rather over 7 inches. On the right side the average is 19·8 cm., and on the left 19·2 cm.

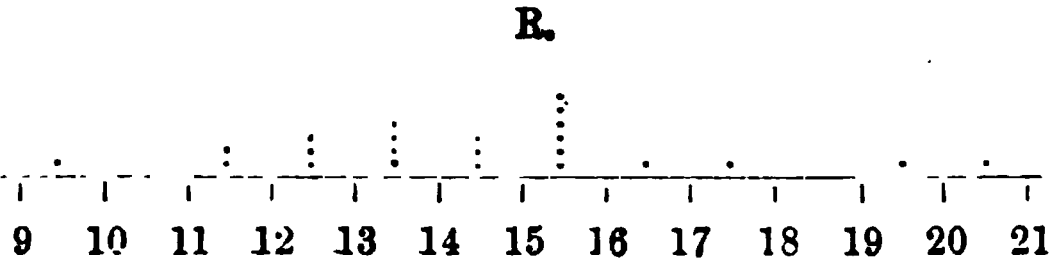
The range of variation is very great, as will be seen from the accompanying table :—

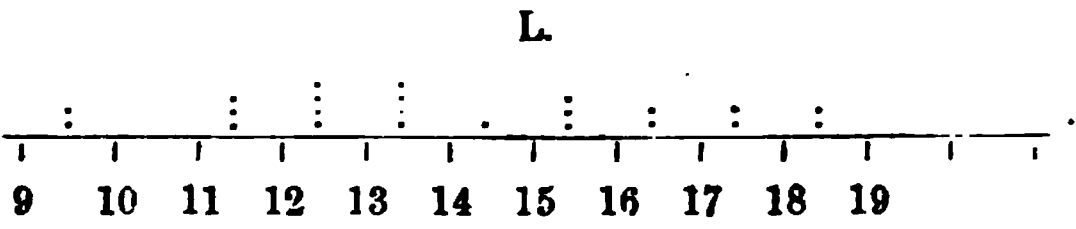
TABLE XIV.—*Distance of Origin of Third Perforating Artery from Poupart's Ligament, in Centimetres.*



The average distance of the origin of the third perforating artery from the bifurcation of the common femoral is 14·3 cm., or rather over 5½ inches. On the right side the average is 14·6 cm., on the left 14·1 cm. The range of variation is given in the accompanying table :—

TABLE XV.—*Distance of the Origin of the Third Perforating Artery from the Bifurcation of the Common Femoral.*





As a rule the third perforating artery pierces the adductor magnus only, but in a certain number of cases, when the artery is higher than usual, or when the adductor brevis is unusually low, it may pierce both adductors.

TABLE XVI.—*Muscles pierced by the Third Perforating Artery.*

|                                       | R.       | L.         |
|---------------------------------------|----------|------------|
| Adductor magnus, . . . . .            | 20 (77%) | 22 (78·6%) |
| Adductor magnus and brevis, . . . . . | 6 (23%)  | 6 (21·4%)  |
|                                       | 26       | 28         |

TERMINAL BRANCH OF THE PROFUNDA.

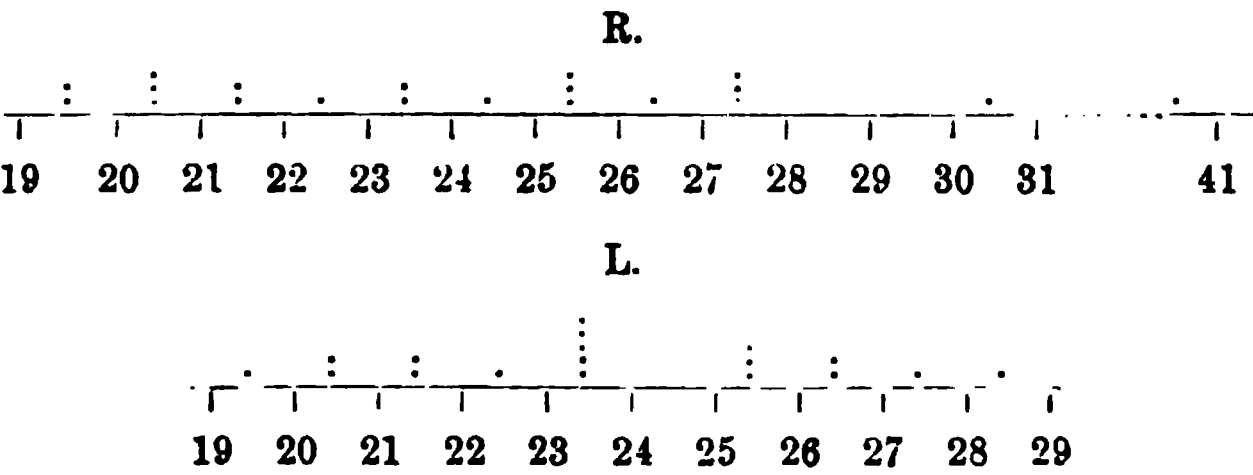
The terminal branch of the profunda is usually the fourth perforating artery, but it may be the third or the fifth, or it may end as a muscular branch in the adductor magnus or gracilis without perforating at all. It is worth while calling attention to the ease with which one of the muscular branches of the profunda which do not really pierce the abductor magnus may be mistaken for an extra perforating artery. The methods in which the profunda femoris ends may be tabulated in the following manner:—

TABLE XVII.—*Methods of Termination of the Profunda.*

|   | R.         | L.         |
|---|------------|------------|
| 1. As the third perforating, . . . . .  | 3 (10·7%)  | 7 (24%)    |
| 2. As the fourth perforating, . . . . . | 19 (69·8%) | 18 (62·3%) |
| 3. As the fifth perforating, . . . . .  | 1 (3·5%)   | 1 (3·4%)   |
| 4. As a muscular branch, . . . . .      | 5 (16%)    | 3 (10·3%)  |
|   | 28         | 29         |

It is difficult to say where the terminal branch of the profunda takes origin, but we have a certain number of statistics on the place where it perforates the adductor magnus. In order to arrive at an average, all those cases have been excluded in which the artery ended in, but did not really perforate, the adductor magnus, and also all those cases in which the third perforating formed the terminal branch of the profunda. Excluding these, there are 38 records—20 on the right and 18 on the left. The average distance of the point where the terminal branch of the profunda pierces the adductor magnus from Poupart's ligament was 24·5 cm., about 9½ inches, or, roughly speaking, about the middle of the thigh. On the right side it was 24·9 cm. from Poupart's ligament, on the left 24 cm. Occasionally the last perforating passes through the opening in the adductor magnus for the superficial femoral artery, and in one case was as much as 41 cm. below Poupart's ligament. The range of variation is very great, as will be seen from the accompanying table :—

TABLE XVIII.—*Distance of the Point of Perforation of the Terminal Branch of the Profunda from Poupart's Ligament.*



SUMMARY.

The result of this investigation may be briefly summed up as follows :—

1. The internal circumflex is usually the first branch of the profunda, and rises just below the commencement of that vessel, 1½ inches from Poupart's ligament.
2. The external circumflex usually rises about half an inch further down.
3. There are usually four perforating arteries, including the terminal branch of the profunda.
4. The first perforating artery usually rises about 5 inches below Poupart's ligament, and 2¾ inches below the origin of the external circumflex. As a rule, it pierces the adductor magnus and brevis.

5. The second perforating artery usually rises about  $1\frac{1}{4}$  inch below the origin of the first, or  $6\frac{1}{4}$  inches below Poupart's ligament. In about three-quarters of the cases it pierces the adductor magnus and brevis.

6. The third perforating artery rises, as a rule, about  $\frac{3}{4}$  inch below the second, or 7 inches below Poupart's ligament. In more than three-quarters of all cases it pierces the adductor magnus only.

7. The fourth perforating artery is usually the terminal branch of the profunda, and pierces the adductor magnus about  $9\frac{1}{2}$  inches below Poupart's ligament, or, roughly speaking, about the middle of the thigh.

8. All the perforating arteries will usually be found in the middle third of the thigh, though the origin of the first is a little higher.

9. Sex seems to exert little or no effect on the origins of the branches of the profunda.

10. The side of the body seems also to have little influence though in many cases it will have been seen that the arteries on the left side come off a little lower than those on the right.

AN AUSTRALIAN SKULL WITH THREE SUPERNUMERARY UPPER MOLAR TEETH. By Prof. Sir WM. TURNER, F.R.S.

I HAVE from time to time recorded cases of supernumerary teeth in man. In this *Journal*, vol. xii. p. 142, I described in a Scotsman a supernumerary incisor situated between the upper central incisors; and in vol. xxvi. p. 60, an African skull, from the Gambia, in which a pair of supernumerary teeth were intercalated in the molar series, opposite and internal to the interval between the 1st and 2nd true molars. Also in my *Challenger Report*, vol. xxix., 1884, an Australian skull in which a tooth occupied a cavity in the palatal plate of the left superior maxilla close to the mesial suture, and another Australian skull in which a supernumerary tooth was placed immediately behind the left upper wisdom tooth.

In July 1899 I received from Dr W. Ramsay Smith of Adelaide, the skull of an old aboriginal Australian, which, owing to the peculiarity in the dentition, he presented to the Anatomical Museum of the University. The left side of the skull showed an extensive comminuted fracture, which was said to have been purposely produced by a blow from a waddy, owing to the man being unable to keep up with the tribe in its migrations. The skull was obtained at Morambro Station, thirteen miles from Naracoorte, in the S.E. of South Australia.

The general characters of the skull were those of an aged man. The cranial sutures were extensively obliterated. In the lower jaw all the molars had been shed some time before death, and the corresponding alveolar border had been absorbed. The incisor and canine sockets were present, though their teeth had been lost before the skull reached me. In the upper jaw the incisors had also dropped out, but the sockets were left, the canines and bicuspid were worn down to stumps, and the true molars were flattened from use on the grinding surface.

Behind the *right* upper wisdom tooth was a shallow socket in which had been lodged a small supernumerary molar.

Behind the *left* upper wisdom were two sockets, in each of which a supernumerary molar was contained. The more anterior of these teeth had erupted, and was directed obliquely backwards, immediately behind the left wisdom. Its crown measured 6 mm. in diameter, both antero-posteriorly and transversely, and it was partly destroyed by caries. It was much smaller than the crown of the proper wisdom tooth, which measured 11 mm. in transverse by 9 mm. in antero-posterior diameter. The fang was single and short, and its socket was simple, like that of the corresponding supplementary molar on the right side. Immediately behind the left supplementary molar was a second additional tooth which had not cut the gum. It was lodged in an alveolus in the tuberosity at the posterior end of the dentary border of the superior maxilla. When the outer wall of the socket was removed, the tooth was seen to be 10 mm. long by 5 mm. in width; the fang was single, and the free surface of the crown, quite unworn, was irregularly cuspidated. The presence of the non-erupted supplementary left molar led me to open into the tuberosity of the right superior maxilla, to see if it also contained a cavity and tooth, but without result, as only the cancellated tissue of the bone was exposed.

From the series of specimens which I have recorded, it is obvious that the upper jaw is much more frequently the seat of supernumerary teeth than is the mandible.



## ARCHÆOLOGIA ANATOMICA.

### VI.

By E. BARCLAY-SMITH, M.D.

#### JOHN HALLE: A SIXTEENTH CENTURY ANATOMIST.

THE "Compendious work of Anatomie, more utile and profitable than any heretofore in the Englyshe tongue publyshed," annexed to Mr John Halle's "A most excellent and learned woorke of Chirurgerie,"<sup>1</sup> is perhaps the earliest anatomical treatise written by an Englishman, and published in England, now existent. Halle is far from being the earliest English anatomical writer of whom we have record. Bartholomew the Franciscan (Glanville?), John the Englishman (Gadesden), William Horman, the vice-provost of Eton, Thomas Geminus, the eminent engraver, and Thomas Vicary, surgeon to four successive sovereigns, all take precedence. Their works, however, were in some cases never published in England; and of the English treatises they are all, with the exception, perhaps, of Vicary's "Profitable treatise of the Anatomie of man's body," mere transcripts from the classical anatomists; Hippocrates, Galen, Avicenna, Vesalius, etc., being directly copied.

Vicary's profitable treatise first saw the light in 1548. In 1577, fifteen years after his death, it was republished by the surgeons of the hospital of which Vicary was such a distinguished member, viz., St Bartholomew's. Vicary, however, has been the victim of the fate which has befallen so many sixteenth century writers. The first edition has, as far as I know, been wiped off the face of the earth; while Dr Furnivall states in his preface to the reprint of the second (1577) edition, published by the Early English Text Society in 1888, that it was made from the unique copy. A second copy of this valuable book made its appearance a few years since in the University Library of Cam-

<sup>1</sup> "A translation of the *Chirurgia parva* of Lanfranc."

bridge, one of the many valuable additions resulting from the Adams bequest.

Our 1565 edition of Halle, though it cannot boast of being much more than a compilation, yet contains many original reflections, and is not a mere translation of the works of the classical anatomists.

How this work first made its appearance is a matter of considerable doubt. James Douglas,<sup>1</sup> whose valuable bibliographical researches have won a greater meed of recognition on the Continent than in his own country, states that Halle published a quarto work of Anatomy, consisting of 96 pages, in London, 1565, with the following title:—

*“A very fruitfull and necessary work of Anatomy, or dissection of the Body of Man, compendiously showing the Natures, Forms, and Offices of every member from the Head to the Feet, with a commodious Order of Notes leading and guiding the Chirurgeon's Hand from all Offence and Error in right way of perfect and cunning operation; compiled in three treatises; more useful and profitable than any heretofore in the English tongue published.”*

Douglas adds that this anatomical treatise is also to be found at the end of Halle's translation of Lanfranc's *Surgery*.

It is somewhat remarkable that, assuming Douglas to be correct in his statement, the anatomical treatise of John Halle should have been published twice in one year. There is some resemblance in the titling of the two works, and further, the anatomical section of the “most excellent and learned woorke” occupies exactly 96 pages, and is compiled in three treatises. I have searched diligently, and I can guarantee that the book furnishes no internal evidence of the anatomical treatise having been published separately. It is possible, of course, that the anatomical section was reprinted the same year, and published with a new title, but of the existence of such a reprint I can glean no direct evidence; the book is not to be found in the catalogues of any of the great libraries. Indirect evidence there is in plenty: the title of the book, usually much abbreviated, is copied from one bibliography to another, and unfortunately not

<sup>1</sup> *Bibliographie Anatomice Specimen*, London, 1715, p. 103.

always, as the sequel will show, with that scrupulous care which it behoves a bibliographer, of all men, to exercise.

I was much puzzled in finding in Watt's<sup>1</sup> list of writers on anatomy, one John Hallaway. I eventually found this title :

*Hallaway. Fruitful and necessary work on Anatomy.*

Compare the foregoing with Haller's<sup>2</sup> entry concerning the same author,

*Hallaway fruitful and necessary work on Anatomy.*

and, finally, Haller's entry with that of Douglas,

*Hall a very fruitful and necessary work on Anatomy.*

and the process of evolution whereby this early English anatomist sprang into existence is obvious. Mind, I do not accuse Mr Haller of being the original culprit, and there are steps in the process of this titular manufacture which I believe are wanting, and which I am endeavouring to find.

The anatomical armament which Mr Halle provides for the youthful surgeon is not very extensive, compendious though he describes his work to be. Whether his book was widely read or not, I cannot say; but it soon withered and died, and subsequent editions were not forthcoming from his publishers. A very different fate from that which befell Vicary. His treatise seems to have been *the* text-book on the subject for at least 100 years, and passed through edition after edition, the ninth making its appearance in 1641.<sup>3</sup>

As far as intrinsic merit is concerned, I think this fate was ill deserved, and that the palm of merit should, of the two, be awarded to Halle. His descriptions, borrowed though they may have been, are in many cases more reliable than those of Vicary, his quotations from classical authorities are more numerous, and he is obviously the more widely read man of

<sup>1</sup> *Bibliographica Britannica*, vol. i. p. 459, and vol. iii. (under subject 'Anatomy').

<sup>2</sup> *Bibliotheca Anatomica*, vol. i. p. 233.

<sup>3</sup> The reason for this is not far to seek. Halle was probably a comparatively obscure provincial surgeon practising at Maidstone, while Vicary was one of the best known surgeons of his day. He was not only the first Master of the Barber Surgeons, but he was attached to the Courts of no less than four reigning monarchs—Henry VIII., Edward VI., Mary, and Elizabeth.

the two. A few extracts, taken at haphazard from the two authors, will serve to support this contention.

Thus concerning the description of the proximal bones of the tarsus:

## VICARY.

Fyrst, next the ankle bone is one, called in Latin Orobalistus:<sup>1</sup> next under that towardes the Heele is one called Calcany: and betwene them is another bone called Os nauculare.

## HALLE.

Unto the Malleoli is knytte a bone called in greke Astragalos, and in latine Talus. Next unto these behind is joynd the hele bone, called of the Grecians Pternan, of the latines Os Calcis, or Calcaneum. Then nexte before is the insteppe bone called (of hys forme) the thiplate bone, and therefore in greke Scaphoeides, and in latine Nauiforme.

The path of exit for the semen is described thus:

## VICARY.

The Yard is an official member: and it hath in it two passages, or principall issues, one for the Sperme, and another for the Urine.

## HALLE.

The fede is carryed to the yarde, and there and thence, throughe the urine passage out of the same, etc. Leaste anye man shoulde judge two passages to belonge to the same: one for sperme, and an other for urine. Yet are there not.

It seems as if Halle must have been acquainted with Vicary's description, as he almost goes out of his way to correct the erroneous impression conveyed by the latter.

Again, Vicary regards the two clavicles and the manubrium sterni as together constituting one skeletal element, while Halle recognised their independence:

## VICARY.

And this cannell bone stretcheth to both the shoulders: One end to the one shoulder, and another to the other, and there they make the composition of the shoulders.

And in the upper end of Thorax is an hole or a concavity in which is set the foot of the Furkle-bone or Cannel-bone.

## HALLE.

In the former parte of the shoulder, is ordained a bone called Clavis, or jugulum, in greke Cleis, and in English ye furcule or canel bone, which is tyed with the broade bone.<sup>2</sup>

Under the throte are ordeined the ii. bones called Claues. And they are fastened at the one end in the shoulder. At the other end they are fastened together with the uppermoste parte of the breft.<sup>3</sup>

<sup>1</sup> Astragalus.

<sup>2</sup> Scapula.

<sup>3</sup> The two descriptions of the clavicle are taken in both cases—the former from the account of the bones of the shoulder (Vicary, p. 49; Halle, p. 60), the latter from that of the bones of the chest (Vicary, p. 56; Halle, p. 66).

Vicary's description of the stomach will undoubtedly appeal to the topographical anatomist, while Halle's will delight the soul of the physiologist.

## VICARY.

It hath the Liver on the right side, chafing and beating him with his lobes or figures: and the Splene on the left side, with his fatnesse and Veynes, sending to him Melancholy, to exercise his appetites: and about him is the heart, quickening him with his Artiers: Also the Braine sending to him a Branch of Nerues to give him feeling.

## HALLE.

The Stomache is called the fyrste vessel, wherein nature maketh and filleth her firste naturalle dygestion. Wherefore it is called the chest or store house, for all the meat belonging to the body, and the cooke also which dresseth meat for all partes of the bodye: for in the bothome of the stomache is made principally the digestion, whereby all the members of the body do growe, and are nourished.

Halle's anatomy is enriched by two full-page woodcuts of the nude male figure, viewed from in front and behind respectively. The engraving is coarse, and the drawing is execrable; but the plates are inoffensive enough. They appear twice, the first time printed on either side of the same sheet, the second time on opposing pages. In my own copy some squeamish vandal eliminated the former, and stuck the latter together with some particularly vile mucilage; while some subsequent curious, but not sufficiently appreciative owner tore the pages apart again with somewhat disastrous results. The copy in the University Library of Cambridge has inscribed on the title-page, "*Hic liber pertinet ad Aulam Barbitonfor ac Chirurgor London ex dono Johis Halle, 156(8?).*"<sup>1</sup> It consequently possesses an additional value in (probably) containing the autograph of the author.

The anatomical treatise forms but a small part of Mr Halle's book. There is much prefatory and dedicatory matter. The surgical treatise is followed by the "Antidotary," a collection of weird prescriptions, and the "Interpretative Table"—a glossarial index of drugs and diseases.

The advice he gives to young surgeons is not confined to the practical work of their subject: he preaches medical ethics and a godly life. No operation of a serious nature must be undertaken without appeal to divine guidance; and he brings

<sup>1</sup> This book belongs to the hall of the Barbers and Surgeons of London, the gift of John Halle. The date is somewhat indistinct, and I am a little doubtful as to whether the final numeral is 5 or 8.

his work to a conclusion with "a praier to be used of the good chirurgeon before he concludes to take in hande the curation of any harde and difficulte thing." This prayer is not remarkable for its brevity. It is to be hoped that strangulated hernias were practically unknown, and that the necessity for performing tracheotomy did not frequently arise in Mr Halle's practice.

Halle was a provincial surgeon practising at Maidstone, and was much vexed in spirit by the peripatetic quacks, soothsayers, and sorcerers for whom Maidstone seems to have been a particularly favourite house of call. Halle apparently suffered both in pocket and reputation at the hands of these gentry, and he uses his book as a vehicle for a round of abuse at their expense—"An historiall expostulation,"<sup>1</sup> as he terms it. He vents his anger in language, if not eloquent, at least forcible, calling his visitors beastly deceivers, hellhounds, devilish beasts, detestable deceiving sorcerers, vile abusers, hellish beguilers, ignorant beasts, ruffians, vagabonds, and by other gentle terms.

His book proves Halle to have been of a loquacious temperament, and his loquacity on one occasion nearly cost him his life.

"There reforted," says Halle, "unto Maydstone one Robert Haris. Well for jestyng a lyttell agaynste the madnes of thys deceauer,"<sup>2</sup> I hadde a dagger drawne at me not longe after. The wordes that I spake were to his hostes, when I fawe him goe by, in this wyse.

Is this (quoth I) the cunyng sothfayer, that is fayde to lye at your house?

Sothefayer, quod she: I knowe no fuche thyng by him, therefore ye are to blame so to name him.

Why, quod I, fuche men and fuche enformed me that he can tell of thynges lofte, and helpe children and cattel bewitched and forspoken, and can tell by lokyng in one's face, what markes he hathe on his bodie, and where, and tell them what they haue done, and their fortune to come.

Yea and all this in dede he can doe, quod she.

Why then he is a Sothefayer and a Sorcerer, quod I.

Well, quod she, yf he haue so mucche cunnyng in his bellye, he is the happyer, and it is the more joye of hym.

<sup>1</sup> Reprinted by the Percy Society; *vide* "Publications," vol. xi.

<sup>2</sup> Deceiver.

Nay, quod I, it were mere folyshnes for hym to carye his cunnyng in his bellye.

And why, quod she.

Why, quod I, thynke you that men of lerning and knowledge carry their cunnyng in their bellies.

Wher els, quod she, and why not.

Mary, quod I, yf he should beare his cunnyng there, he should alwayes waste it when he went to the priuie, and so in time he should lose all his cunnyng.

Thys beyng merylye spoken: turned me afterwards not to a litle displeasure, even at their handes, where I had deserued and loked for friendship as of dutie."

Halle, like many of the medical writers of his age, was bitten with an inexpressible desire to sing. He bursts into poetry on the slightest provocation. The following effusion, sounder, perhaps, in its advice than in its metre, may serve as a fitting conclusion to this review.

" But chieflie the Anatomye  
Ye oughte to understande :  
If ye will cure well anye thinge,  
That ye doe take in hande.

For by the fame aboue the rest,  
Ye shall greate fame deferue,  
The life of man from manye streightes,  
To saue and well preferue.

without the knowledge of whyche arte,  
thou canste not chose but erre :  
In all that thou shalte goe aboute  
Thy knowledge to preferre :

As if ye cutte or cauterize,  
Or use Phlebotomye :  
Ye can not but erre in the same,  
without Anatomye.

He is no true Chirurgien  
That can not shewe by arte,  
The nature of eurye member,  
Eche from other aparte.

For in that noble handye worke,  
There dothe nothings excell,  
The knowledge of Anatomye,  
If it be learned well.

Endeuoure therefore by all meanes,  
The same to knowe and cunne,  
For when thou haste it perfectlye,  
Thine arte is halflye wunne.

For thereby shalt thou understande,  
Of eche member in dede,  
Their nature and their offices,  
And howe they doe procede.

And unto what good use they serue,  
As well the leaste as moſte,  
And by their hurte Prognosticate,  
what action will be loſte.

whereby of knowledge and greate ſkill,  
Thou shalt obtaine the brute,  
And men to thee in generall,  
For helpe shall make their fute.

wherefore all honour, laude and praise,  
To God aſcribed be,  
The Father, Sonne, and holye Ghoſte,  
One God and perſonnes three."



## Notices of New Books.

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*Le Système Nerveux Central, Structure et Fonctions, Histoire Critique des Théories et des Doctrines*, par JULES SOURY. Paris : G. CARRÉ et C. NAUD. 1899.

THE impetus given in France to the study of the Nervous System by the anatomical, pathological, and clinical writings of the late Dr Charcot, and by the comparative anatomical investigations of the late Professors Gratiolet and Paul Broca, has not been exhausted by the deaths of these eminent men. In our twenty-ninth volume we called attention to the first volume of an important treatise on the Anatomy of the Nerve Centres, by Dr J. Dejerine and his accomplished wife, which from the clearness of the description, and the beauty of the illustrations, constituted an important contribution to our knowledge of this difficult department of anatomical study.

During the year 1899, Dr Jules Soury has published the elaborate treatise named at the head of this article. The first part consists of a summary of the progress of knowledge of the structure and functions of the organs of life and of sensibility and thought from the time of the early Greek authors to the present day, as developed in the writings of anatomists, physiologists, and mental philosophers. Like the greater number of scientific treatises in the French language, it is written in so lucid a style that it can be perused with ease and pleasure ; but in addition, it shows the author to be well acquainted with the modern literature of the subject in other languages than his own, and frees him from the reproach, not unfrequently levelled at his compatriots, that they are only acquainted with the work done by their own countrymen.

In the second part of the treatise, which deals with the researches and ideas of contemporary writers, Dr Soury emphasises the necessary relations of function with structure. He calls attention to the importance of distinguishing between the rhinencephalon and the pallium. He describes the sensory and motor paths ; the connections of the divisions of the brain with each other and with the spinal cord ; the central origins of the cranial nerves ; the association and commissural systems of fibres ; the structure and relations of the cerebral cortex in the different lobes ; the localisation of cortical centres ; and the structure and connections of neurons, sensory, and motor involuntary and voluntary. The part taken by successive observers in the investigations which have been conducted on the numerous and difficult problems, physiological and psychological,

comprised in the study of the inner anatomy of the nervous centres, is analysed, and the theories and deductions which have been advocated from time to time are explained and criticised. The reader will find in this elaborate work, extending to 1863 pages, a mass of orderly arranged information on the subjects of which it treats, such as cannot be obtained in any other single book with which we are acquainted.

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*Erinnerungen aus Meinem Leben*, von A. KÖLLIKER. Leipzig: Engelmann, 1899.

IN this volume, which he dedicates to his family, his friends and his colleagues, Professor Albert von Kölliker records the labours of a well-spent life.

Since 1841, when he published his first work on the Spermatozoa of Invertebrate Animals, he has been continuously engaged in anatomical research, chiefly histological and embryological, and in the consideration of the physiological problems which have had a bearing on his anatomical studies. His text-books on histology and embryology, and his separate memoirs on a wide range of human and comparative anatomy and physiology, amounting collectively to 245 distinct publications, constitute a mass of original work such as falls to the lot of few men to execute, and will serve to keep his memory green for all time in the annals of biological science. But Professor Kölliker's activity has not expended itself in minute research. For 57 years he has been engaged in continuous teaching. In 1842 he was appointed Prosector to Henle, then Professor of Anatomy in Zürich; and in 1844 Extraordinary Professor of Anatomy and Physiology in the same University. In 1847, when thirty years of age, he was called to Würzburg, the University of which city he still adorns after a service of fifty-two years. He is a living example of the possibility of combining in one person great activity as a teacher, with a power of applying himself to independent enquiry, during more than half a century. We may feel confident that his teaching has been vitalised, and had a freshness imparted to it by his constant appeals to nature, as he communicated year by year to his pupils the results of his own observations.

In giving the title of his memoirs, and their date and place of publication, Professor Kölliker appends to the most important a brief *resumé* of the contents, which enables the reader to ascertain in an easily accessible manner the chief facts of which they treat, and the conclusions derived from them.

The earlier part of the volume contains an account of the leading events of his career. We read how he attended carefully to the preservation of his health by physical exercise. In his early life he was a gymnast, fond of swimming and riding, and a great pedestrian. In later years he was a keen sportsman, and frequently occupied the autumn vacations in travel, so that he has been able to preserve both

bodily and mental activity and vigour throughout a long and laborious life. He has printed a number of letters, written to members of his family when on his travels, of which those relating to his visits to England and Scotland, where he had many warm personal friends, are especially interesting. The writer of this notice, then a first year's student at St Bartholomew's Hospital, recalls an incident, not referred to in the letters, associated with Professor Kölliker's visit to London in 1850. At that time the classical memoirs published in 1846 and 1849, on the structure and distribution of the smooth or involuntary muscles, were attracting much attention. Sir James Paget, then the Lecturer on Physiology and General Anatomy at St Bartholomew's, had been explaining one day to his class the importance and significance of these observations, when on subsequently going to the operating theatre, we were told that Professor Kölliker was present. As it happened, the operation was an amputation of the leg, and, as soon as the leg was removed, Mr Paget exposed the long saphenous vein, and along with Professor Kölliker demonstrated the contractility of its muscular coat, an incident not likely to be forgotten by those who were present. All anatomists wish a continuance of life and vigour to this Nestor of our profession.

W. T.



# Journal of Anatomy and Physiology.

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ON SEPARATE ACROMION PROCESS. By JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's College, Belfast.*

NEARLY all our anatomical and surgical museums contain specimens of scapulæ in which part of the acromion process is separated from the rest of the bone. As a rule, these preparations have been macerated and dried, and have no history attached to them. Under such circumstances it is not surprising to find that curators of museums have experienced some difficulty in deciding as to whether these specimens are cases of non-union of the acromion epiphysis, or true fractures of the acromion process which have failed to unite.

It is unnecessary to attempt any summary of the literature on this subject, or to enter into any elaborate discussion of the points in dispute, as this has recently been done by the late Sir John Struthers.<sup>1</sup> My object is rather to place on record notes of the dissections of several specimens which I have had the opportunity of examining. As we are mounting a type collection of fractures in the Surgical Museum of the Queen's College, Belfast, and naturally wish to have the series as complete as possible, all the subjects dissected in the anatomical department during the present winter session have been examined for fractures with more than usual care. From 40 subjects no less than 5 scapulæ have been obtained, in which the acromion process was separate from the rest of the bone. Of course these numbers are too small to justify any conclusion as to the average frequency of occurrence of this condition, but they are of interest

<sup>1</sup> "On Separate Acromion Process," *Edinburgh Medical Journal*, October 1895, April 1896, June 1896, and August 1896.

in connection with the experience of Mr Arbuthnot Lane,<sup>1</sup> who found fracture of the acromion the commonest of all fractures met with in a large number of subjects dissected in the medical school of Guy's Hospital. My five scapulæ were obtained from three subjects. In a male aged 31 years, and in a female said to be 81 years of age, the condition was bilateral, and in a female aged 70 only the right scapula was affected.

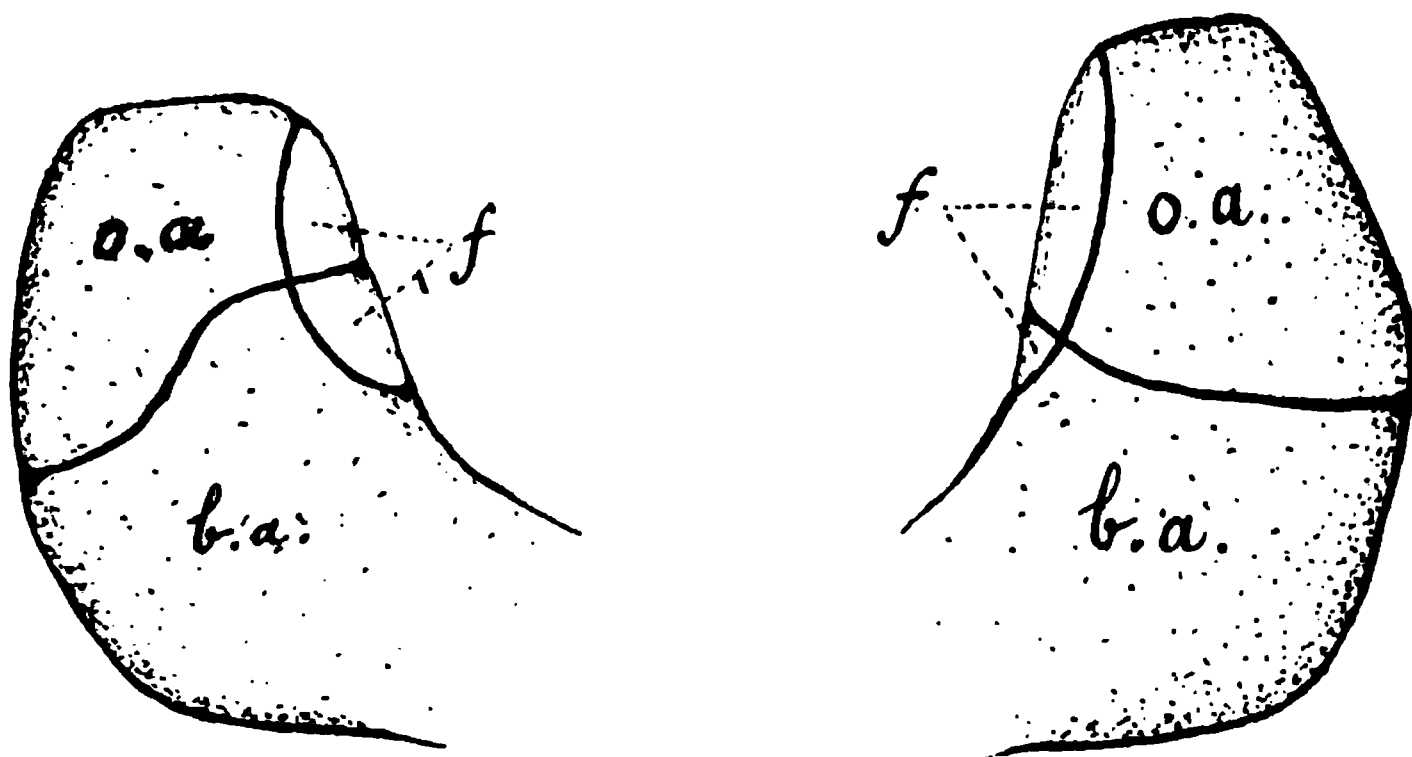
CASE 1.—Male, æt. 31. Right scapula. The bone was well developed, and the clavicular facet on the acromion  $\frac{7}{8}$  of an inch long. The line of separation between the base-acromion and the os acromiale (see fig. 1) commenced on the inner side  $\frac{1}{8}$  of an inch in front of the posterior end of the clavicular facet, and passed outwards nearly at a right angle with the long axis of the acromion, reaching the outer border of this process a little behind a point midway between its anterior and posterior extremities. The opposing surfaces of the two bones were slightly thickened. Union was effected by means of a well-developed diarthrodial joint; the capsular ligament was strong, the articular surfaces covered by a thin layer of cartilage, and the synovial membrane was freely continuous with that of the acromio-clavicular joint. The movements permitted at this abnormal joint were about as extensive as those between the clavicle and the acromion. The os acromiale was quadrate, but broader behind than in front. Its posterior border was an inch long, and the distance from the middle of this border to the anterior extremity was also an inch.

CASE 2.—Left scapula of same subject as Case 1. The general form of the scapula and the structure of the intra-acromial joint were practically identical with the condition of the right side. The line of separation, however, between the two parts of the acromion crossed the clavicular facet almost exactly midway between the two ends (fig. 2). It passed for a quarter of an inch directly outwards, and then turned outwards and backwards, joining the outer border, as on the right side, a little behind its middle. This os acromiale, therefore, was not quite as large as the right one. Its base, where it articulated with

<sup>1</sup> "Some Points in the Physiology and Pathology of the Changes produced by Pressure in the Bony Skeleton of the Trunk and Shoulder Girdle," *Guy's Hospital Reports*, vol. xliii., 1886.

the basi-acromion, measured 1 inch across, and its antero-posterior extent was  $\frac{3}{4}$  of an inch.

CASE 3.—Right scapula of female, aged 81 years. Muscular impressions on bone well marked. Acromion process of the quadrate type, with distinct posterior and antero-lateral angles (see fig. 3). The os acromiale was an inch broad at its base, and measured  $\frac{3}{4}$  of an inch from the middle of its base to its anterior extremity. The intra-acromial joint was provided with a capsular ligament and a distinct synovial cavity. The opposing osseous surfaces were uneven, and that of the basi-acromion was convex from side to side, the os acromiale



FIGS. 1 and 2.—Acromion processes of right and left scapulæ of a man aged 31 years. *o.a.*, os acromiale; *b.a.*, basi-acromion; *f.*, facet for clavicle.

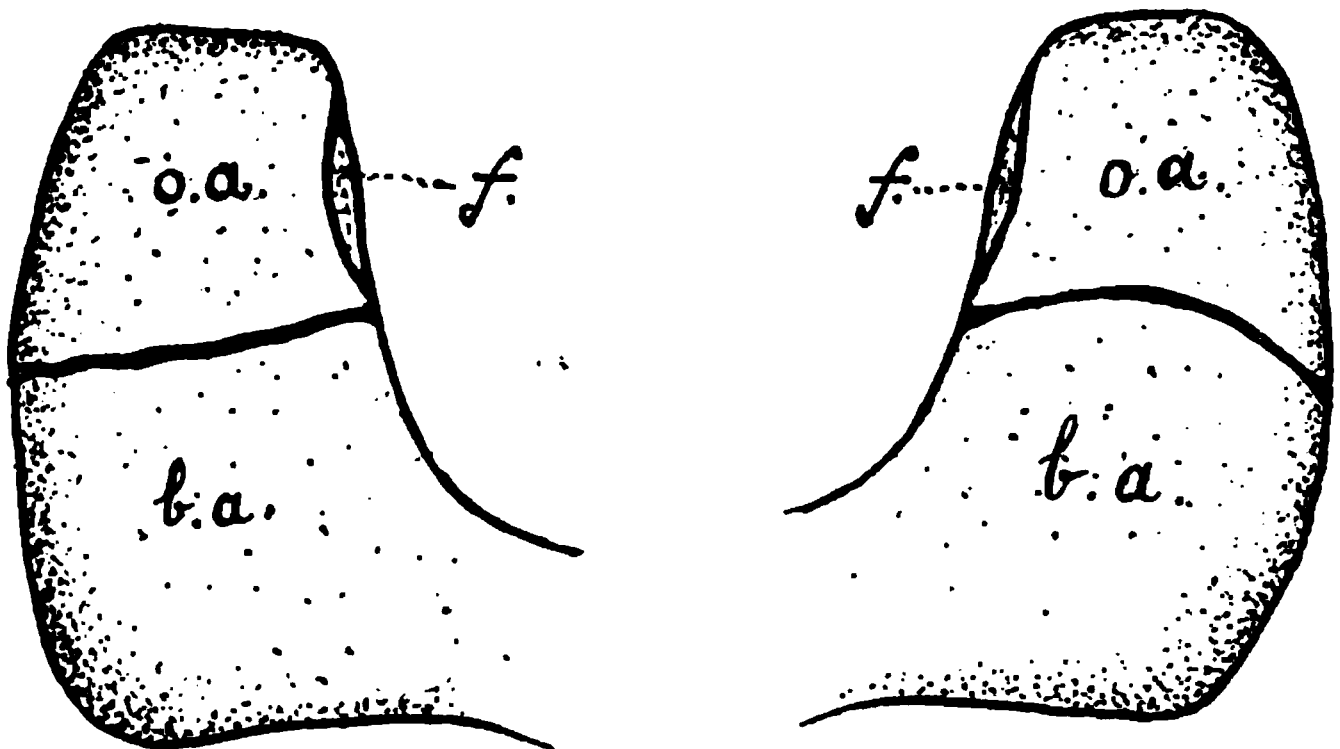
presenting a corresponding concavity. The layer of articular cartilage was very thin, and appeared in some places to have undergone a fibroid change. Internally the line of articulation was just posterior to the acromio-clavicular joint, and on the outer side midway between the two ends of the outer border.

At the acromio-clavicular joint the articular surfaces were very small and ill-defined, and the space between the two bones was occupied mainly by fibrous tissue.

CASE 4.—The condition of the left scapula and the structure of the intra-acromial joint were similar to those found on the right side. The line of articulation was straighter, and the os acromiale nearly  $\frac{1}{4}$  inch longer than on the opposite side, but the intra-acromial joint had the same relation both to the

acromio-clavicular joint and to the outer border of the acromion (see fig. 4).

CASE 5.—Right scapula of female, aged 70 years (fig. 5). The general shape of the acromion process was falcate rather than



FIGS. 3 and 4.—Acromion processes of right and left scapulæ of a woman aged 81 years. Lettering as in fig. 1.

quadrate. The os acromiale was somewhat triangular in form. Its line of junction with the basi-acromion commenced on the

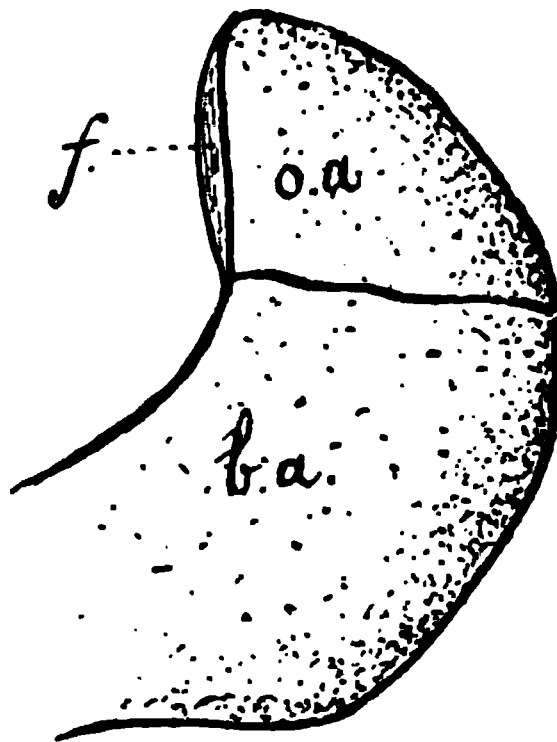


FIG. 5.—Acromion process of right scapulæ of woman aged 70. Lettering as in fig. 1.

inner side immediately behind the acromio-clavicular joint, and passed outwards and a little backwards. The structure of the intra-acromial joint was similar to that of cases 3 and 4.



The most important points in these cases are the following:—

- (1) That in two of the three subjects the condition was bilateral.
- (2) That the separate bony element corresponded to the usual form of the acromial epiphysis.
- (3) That in all the specimens the abnormal joint was diarthrodial in character, having a distinct cavity and a capsular ligament lined by synovial membrane.
- (4) In the young man the cavity of the intra-acromial joint was freely continuous with that of the acromio-clavicular joint, and the latter was normal.
- (5) There was no disease of the shoulder joint in any of these cases, and no signs of fracture of the clavicle or humerus.

The frequency with which cases of separate acromion process are bilateral has not been definitely determined. Many of the specimens in our museums are without a history, but frequent references to its bilateral occurrence will be found in surgical literature. The statement in Henle's *Handbuch der Anatomie*, Dritte Aufgabe, Bd. i. s. 236, that "Die Anomalie scheint in der Regel auf beiden Seiten zu bestehen" is probably correct, and, if such be the case, it seems to me to favour very strongly the separate epiphysis theory. Of course, both fractures and dislocations may be bilateral, but they are undoubtedly of rare occurrence.

Professor A. Macalister<sup>1</sup> has shown that the ossification of the acromion process is subject to considerable variations, both as to the number of its centres and their form. The most usual condition is that the small metacromial centre joins the basal portion of the acromion, and the other centres fuse together to make a common epiphysis, which is situated in front of a line passing from near the posterior part of the clavicular facet to about the middle of the outer edge of the bone. Apparently, in the majority of cases, the epiphysial line is placed just posterior to the clavicular facet, but in three young scapulæ in my possession it divides this facet, as in Case 2, into two nearly equal parts. The bases of the separate acromion processes, in the cases described above, closely correspond to the usual epiphysial

<sup>1</sup> "Notes on the Acromion," *Journal of Anat. and Phys.*, vol. xxvii.

line in young bones. My experience, however, agrees with that of Macalister, who says that "Out of the 45 cases of this condition which I have examined I have never found the metacromion attached to the ossicle." This is probably due to the fact that when the metacromial centre joins the other acromial epiphyses, the line of union of the common epiphysis with the base of the acromion being more curved and irregular, the risk of separation is less. I have two young scapulæ in which the epiphysis includes the metacromion. In these the epiphysial line passes from the clavicular facet first outwards, and then turns backwards nearly parallel with the outer edge of the acromion, and terminates at a point a little internal to its posterior angle. Such specimens are obviously better able to resist strains in various directions than those in which the epiphysial line is nearly straight.

As already stated, in all my specimens the separate acromion process was connected with the basi-acromion by a diarthrodial joint, and Struthers found a similar arrangement in six moist specimens which he dissected. The joint between the scapula and its acromial epiphysis is normally a synchondrosis. In the separate epiphysis theory we may assume that owing to repeated slight strains, or to one of greater force, a cavity is formed in the cartilage, and a typical diarthrodial joint gradually developed. On the hypothesis of a fracture of the fully ossified bone, it is difficult to explain the presence of a layer of cartilage on the opposed surfaces. Struthers describes a thin layer of articular cartilage as being present in all his specimens. In most cases this cartilage had undergone some softening, but that is not surprising, as all his cases were from subjects about 80 years old, except one of 64. Three of my five specimens were from females 70 to 80 years old, and in these I was not able to fully satisfy myself that the material covering the joint surface was really articular cartilage. In the two cases, however, from a male 31 years of age, the cartilage was typical, and identical with that of the acromio-clavicular joint. The general condition of the intra-acromial joints in this subject appear to me to be inexplicable on the fracture of ossified acromion theory.

Mr Arbuthnot Laue advocates very strongly the fracture hypothesis, and gives (see *loc. cit.*, p. 419) six reasons in support

of his contention. The first three are the frequency with which it is associated with other fractures of the shoulder joint, or with rheumatoid arthritis, and its great frequency on the right side. The specimens described by Struthers and myself afford no support to these statements, and Lane appears to ignore the fact that it is often bilateral. The other reasons advanced are the variation in the line of supposed fracture, and the fact that they correspond in situation to fractures produced experimentally after death. Struthers, although he rejects a number of the arguments advanced by Lane, yet sums up his own views as follows:—"The epiphysis theory is attractive to the anatomical mind, and it is not easy to part with the impressions of one's earlier years in the dissecting-room, but when the evidence is critically examined, it has to be abandoned for the fracture theory" (*Edin. Med. Journ.*, Aug. 1896, p. 106).

The support given to the fracture theory by Arbuthnot Lane and Struthers is certainly not shared by anatomists generally. Thus Macalister in his paper on the acromion process already referred to writes:—"The condition of the persistently separate os acromiale, which I have found in fifteen out of a hundred scapulæ taken at random, is due to the preacromial and mesacromial centres, and the persistence of their separation from the base of the spine, and from the metacromial centre which always consolidates with the base" (p. 249).

Struthers appears to consider that the epiphysial line of the acromion is very constant in its position, and he supports the epiphysis theory mainly because his specimens showed some variation in the line of separation, and especially on account of the fact that this line passed from just behind the clavicular facet nearly transversely outwards, whereas the epiphysial line is directed outwards, with a considerable inclination backwards. The extensive observations of Macalister prove that the views of Struthers on the normal ossification of the acromion were based on the examination of too limited a number of young scapulæ.

The line of union of the epiphysis of the acromion, formed by the union of the centres in front of the metacromion epiphyses, may be nearly transverse to the long axis of the acromion, or directed backwards and outwards, and specimens of separate

acromion show a similar variation. The neighbourhood of this line is a weak part of the acromion process, and can, as Arbuthnot Lane has shown, be easily broken in the dead subject by a direct blow with a small hammer. It is quite conceivable that such fractures may occasionally occur in the living body, although they are very rarely diagnosed by surgeons. That such accidents should be very common, often bilateral, and fail to unite, is extremely improbable.

A CONTRIBUTION TO THE ANATOMY OF THE DIGESTIVE TRACT IN SALMO SALAR. By J. KINGSTON BARTON, M.R.C.P. (*From the Jenner Institute.*) (PLATES XL-XLIII.)

It has been stated (see "Life-History of the Salmon," Scotch Fishery Board, 1898) that when salmon enter our estuaries there has begun an extensive desquamative catarrh of the mucous lining of the intestines which spreads upwards to the stomach (see pages 16, 20, and 21 of above Report). Dr Lovell Gulland, who is responsible for the microscopic examinations made in the Laboratory of the College of Physicians of Edinburgh for this Scotch Report, states that for uniformity he placed every specimen in saturated perchloride solution.

In the course of my observations it was found that on treating the stomachs of grilse and sea trout in this way, the appearances of a shed epithelium was noticed. But on treating the stomachs and pyloric tubes of cod and whiting, and stomachs of smelt in the same way, it was found that these fish also exhibited the appearances of a universal desquamative catarrh.

These fish were in perfect health, as shown by the condition of the foods in the stomach and intestines, yet under the microscope the mucous epithelium was shed, and that of the submucous glands also freely separated and shrunk.

In November, whilst fishing in the river Fowey, I secured two cock salmon and one sea trout. Within a few hours of capture the stomach of one salmon and also that of the sea trout were well washed in tap water, and then placed in equal parts of alcohol and  $\frac{1}{2}\%$  solution of chromic acid, remaining in this four days. The stomach of the other salmon was dilated with a similar solution, the pyloric appendages and a part of the small intestine being dilated at the same time. This injected specimen was kept in the solution six days; then all were prepared in the usual way for imbedding in paraffin, the sections being stained afterwards with hæmatoxylin and eosin.

Let me here state that I carried out the microscopic work in the Laboratories of the Jenner Institute under the supervision of Professor Macfadyen, and assisted by his staff.

The transverse section of the pylorus reveals the most perfectly natural epithelium (fig. 3). Now this fish was a red salmon, not yet on the spawning beds, but in the higher reaches of the river. Dr Gulland maintains that when the salmon has gained the higher reaches of the river the catarrh has far advanced throughout the digestive tract.

A section of the small intestine shows the epithelium quite normal, disturbed perhaps in places, but this is clearly due to difficulties in section cutting. A section of the cardiac part of stomach of the second salmon also shows perfectly normal epithelium, and not the slightest evidence of a desquamative catarrh. This single specimen is really conclusive of a serious fault in the preparations of the Edinburgh Laboratory, and indicates an error in the deductions drawn from them. For this particular salmon was so red and discoloured that he must have been weeks or perhaps months in the river. The thinness of the fish as compared with his length, indicated a long residence in the fresh water. The milt was within a very few weeks of full growth.

The sections from the sea trout show normal mucous epithelium, yet this fish had also been in the river a long while. Sea trout evidently do not feed when once settled in the rivers, and have all the same characteristics in this matter of non-feeding as is found in *Salmo salar*.

The majority of the specimens examined in Edinburgh were received in the warmer months, and there can be no doubt the mucous material found in the stomachs of these and all fish very quickly undergo post-mortem changes which accelerate this condition of a shed epithelium. In the comparatively functionless stomach of the salmon it is apparent that the epithelium would be more easily affected than in healthy fish in spite of the more active gastric juice of the latter. It is well known that when the percentage of HCl is below a certain point, bacteria thrive more vigorously in the digestive tract. This would be a further stimulus to rapid changes in the epithelium after death, and consequently explains why the changes are more marked in

salmon than in trout or other vigorous fish. Dr Noël Paton's Report proves conclusively that there is great diminution in the amount of HCl in the gastric juice of salmon. Further, he also proves there is some very active zymogen in the mucous membrane of the intestines and appendages of salmon. This, doubtless, would be a potent factor in the rapid alteration of the epithelium after death, noted in this particular part of the digestive tract.

Nearly two hundred salmon were examined carefully by me this year (macroscopically), and it was very marked, as summer advanced, how much like the results of a purulent catarrh the contents of the stomach appeared. The fresher the fish the less marked the signs appeared. In all these fish the pyloric part of the stomach was, as a rule, quite contracted, and in this part the appearance was much more healthy-looking. Only in the very hottest days did the contents become like that of purulent catarrh throughout the entire digestive tract. The interior of the stomachs of whiting and cod which had not recently been feeding, and which had been out of the sea at least thirty hours, also present this aspect of a mucous catarrh, and a contracted rugose state of the walls of the stomach. In preparing specimens of these whiting for the microscope in alcohol with chromic acid solution the epithelium of the gastric glands is well seen, but shed from the basement membrane, and the superficial columnar epithelium is entirely shed. This is clearly due to post-mortem changes. The catarrhal appearances are more marked when the specimens are fixed in saturated perchloride or 10% formalin solutions.

There is no question the gastric juices of a fish are very potent. On opening one salmon this spring I found the stomach dilated to its full with six large-sized herrings, that nearest the salmon's mouth being barely changed in appearance, whilst the sixth had only its spinal column undigested, those in between being in a graduated state of digestion, and yet all these fish were in the one cavity. The rugæ had entirely disappeared, and the wall of the stomach was extremely thin. In the intestines of this fish, which were very full of faecal matter, it was noticeable how very little there remained of any fish bones, showing how solvent are the gastric juices. In a good many other fish the

spinal columns of herring were found, but never beyond the region of the duodenum. As a matter of interest, it may be stated that both in salmon and sea trout the food fish is always swallowed tail first.

If a normal section of the digestive tract of a fish is to be obtained, the specimen cannot be too fresh. As soon as possible all the mucous material should be gently washed away, and the specimen at once placed in the fixing solution. Alcohol with  $\frac{1}{2}$  to 1 % of chromic acid solution, equal parts, seems to give the best results.

It seems difficult to believe that a salmon entering the river in the splendid health it does should be suffering from an acute desquamative catarrh, and more especially beginning at the hinder end of the canal. It would be more reasonable to suppose that after a long residence in fresh water such a condition might possibly arise; but the examination of my old red fish quite refutes both suggestions. It is quite certain that the methods employed in Edinburgh have misled the observers.

Dr Gulland states that the stomachs of trout treated in their perchloride method reveal no such signs of catarrh. Although the outward view of a trout's stomach and intestines is but a miniature copy of that of a salmon, yet its interior differs in some important details. As a rule, a trout feeds on flies and small water-insects, and even when the stomach is fairly full the stomach is somewhat contracted and rugous; but, usually, with very little gastric mucus, hence there is very much less chance of post-mortem changes. It is only when a trout is stuffed with worms in flood time that the stomach walls are very thin and distended, and then there is much gastric mucus. Again, when a brown trout fasts it does so only temporarily, but the salmon who reaches our rivers has begun a long physiological fast, and we cannot expect the epithelium of its digestive tract to be as resistant to the effects of post-mortem changes and also to such strong reagents as saturated perchloride and strong formalin.

No doubt, if the delicate physiological test stains were used, it would be found that the epithelial cells both of the mucous surface and of the gastric and intestinal glands would not present a normal functional condition. The physiological fast of the salmon in fresh water would lead one to expect such changes



in the mucous epithelium. The careful experiments in Dr Noël Paton's Reports show how feeble the peptogenic powers of the upper part of the digestive tract in salmon become when the fish enter the rivers.

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## DESCRIPTION OF PLATES.

### PLATE XL.

Fig. 1. Section through the stomach, near pylorus, of a male salmon caught with rod and line in river Fowey, Nov. 23, 1899. Under object-glass  $\frac{1}{4}$ ". This fish was very discolored from a probable many months' residence in a deep hole in the river. The epithelial layer is very perfect. The fish was nearly ready for spawning, its milt being very large.

Fig. 2. The same as fig. 1, but under  $\frac{1}{8}$ ". These two specimens convincingly prove that there is no desquamative catarrh of the stomach in a fish which had been many weeks or months in the river.

### PLATE XLI.

Fig. 3. Cross-section of the pylorus of a male salmon taken Nov. 21, 1899, river Fowey. Under  $\frac{1}{4}$ ". This fish, although red, looked like an autumn-run fish, and possibly had only been up a few weeks. The epithelial and glandular cells are very perfect.

Fig. 4. Cross-section of the stomach of a smelt in the act of digesting a shrimp  $\frac{1}{8}$ ". A false catarrhal appearance, due to post-mortem changes (as specimen was not obtained until a good many hours after capture), and also to effects of fixing reagents and section-cutting.

### PLATE XLII.

Fig. 5. Section of mid-stomach of same salmon as fig. 3. This stomach had been distended with the fixing solution (alcohol and  $\frac{1}{2}$ % chromic acid). Under  $\frac{1}{4}$ ".

Fig. 6. Same as No. 5, but under  $\frac{1}{8}$ ". The superficial and glandular epithelium is beautifully distinct. But it has not stained well. The columnar epithelium has an attenuated look, possibly due to the abeyance of function during the fish's fast in the fresh water. Yet the epithelial cells are in perfect position. It should be noted that fig. 3 represents the pylorus of this same fish, and yet its cells have taken the stain well.

### PLATE XLIII.

Fig. 7. Cross-section of a pyloric tube of the same fish as fig. 3, under 1". Although the whole of the columnar epithelium stands apart from its basement membrane, it is quite apparent this is only

due to mechanical separation in preparation and section-cutting. The epithelial cells are quite perfect individually and collectively, and no evidence whatever of any desquamative catarrh. Supposing this separation were due to disease, or even to a simple moulting, then the epithelial cells would be broken up and degenerated in various degrees. But it is evident the whole of the epithelium was alive and well up to the moment of death.

Fig. 8. The same as fig. 7, under  $\frac{1}{8}$ ". These last two figures are from photo-micrographs.

The first six figures are from drawings made from photo-micrographs corrected by filling in details from the microscope.

Fig. 1.

Fig. 2.



Fig. 3.



Fig. 4



Fig. 5.

Fig. 6.





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FIG. 7.

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FIG. 8

MR. J. K. BARTON ON Digestive Tract in *Salmo Salar*.



THE JOINTS OF MAMMALS COMPARED WITH THOSE  
OF MAN: A COURSE OF LECTURES DELIVERED AT THE  
ROYAL COLLEGE OF SURGEONS OF ENGLAND. By F. G.  
PARSONS, F.R.C.S., *late Hunterian Professor*.

PART II.—JOINTS OF THE HIND LIMB.

THE HIP JOINT.

SOME of the chief points which attract attention in the hip joint of man are the three thickened parts of the capsule called the ilio-femoral, ischio-femoral, and pubo-femoral ligaments, as well as the intra-articular ligamentum teres running from the bottom of the acetabulum to the head of the femur, and otherwise free in the interior of the joint. In the anthropoid apes the same thickenings of the capsule are found, and it is even said<sup>1</sup> that they are somewhat more prominent than in man. There is no doubt that the ligamentum teres is constantly present in the gorilla, chimpanzee, and gibbon, and it is a most remarkable thing that it is usually absent in the orang. In this museum there are the hip joints of two orangs, in one of which there is a fossa on the head of the femur where the ligament, if it had been present, would have been attached, while in the other specimen there is no such mark. In both these preparations the cotyloid notch and transverse ligament are present as in man.

In the lower or cynomorphine monkeys the ligamentum teres is always present, and resembles the same structure in man, though it seems almost certain to me that it can never be put on the stretch. The three thickened parts of the capsule are present, but are not so well defined as in man; the ilio-femoral band can easily be made out, but its Y-shaped appearance is not evident; I believe that its prominence in the higher apes and monkeys must be a physiological result connected in some way with the conversion of the hind limb from a supporting to a

<sup>1</sup> Keith.

brachiating organ, since, as we shall see, it is not present in lower mammals. It can hardly be an adaptation to the erect position, since in the anthropoids the line of the centre of gravity of the body does not fall behind the centre of the hip joint, as in man, and the semi-erect position is assisted by the contact of the knuckles with the ground. In man, however, it undoubtedly assists in maintaining the erect posture. I have been unable to find any evidence to support Bland Sutton's ingenious suggestion that it is in any way connected with the presence or absence of the gluteus quartus (ventralis). The only proof that the ilio-femoral band is a degenerated gluteus quartus which would be at all convincing to me would be to see one or more human subjects in which the gluteus quartus is present and the ilio-femoral ligament absent, though how the erect position would be maintained in such a case I do not know.

In the lemur the hip joint corresponds with that of the lower monkeys, and the ligamentum teres is present and well marked. In the Cheiroptera the fruit bat (*Pteropus*) has the hip twisted in such a way that the original front of the knee looks backwards and outwards and the plantar surface of the foot forwards. The lesser trochanter is therefore on the outer side; it is situated inside the capsule of the joint, and has an articular summit. When the foot is moved toward the mouth, *i.e.* when the hip is flexed and abducted, this trochanter comes in contact with an articular surface just above the acetabulum, reminding one somewhat of the antitrochanter of birds. There is a well-marked ligamentum teres, which is short, though it never appears to be put upon the stretch. Anyone who has watched a fruit bat taking a grape or other fruit will readily see that this twisting of the hip is an adaptation to allow the knee to flex forward and the foot to be brought into contact with the mouth; the foot in this way is able to take the place of the hand, which in this case has been converted into an organ of flight. In the insectivorous bat (*Plecotus*), the need of using the foot as a hand is not so great, and we do not find the hip so completely twisted round as in the fruit bat; indeed, the knee looks more outward than backward, and the lesser trochanter does not articulate with the ilium. As in *Pteropus*, the ligamentum teres is well marked.

In the Insectivora, both the mole and the hedgehog have no ligamentum teres: the latter is one of several instances which cause me to doubt the universal validity of Bland Sutton's statement that "those mammals in whom a ligamentum teres is absent also lack a gleno-humeral band," because the hedgehog certainly does possess a gleno-humeral band.

In the Carnivora, as in most of the lower mammals, the capsule of the hip is not specially thickened at any one point; the ligamentum teres, however, is thick and well marked in the land Carnivora, at least it is so to my knowledge in the Felidæ (cat, leopard, lion), Viverridæ (civet, genet, ichneumon, and suricate), Hyænidæ (*Hyæna striata*), Procyonidæ (*P. lotor*), Canidæ (dog and fox), Ursidæ (black bear), and Mustelidæ (polecat, stoat, weasel, and otter). It is stated to be absent in the sea otter (*Enhydra marina*), though it is certainly present in the common otter (*Lutra vulgaris*). It is absent in the walrus (*Trichecus rosmarus*) and the seal (*Phoca vitulina*), which are the only two specimens of the aquatic carnivores (Pinnipedia) I have observed.

In the Ungulata, the horse, as Bland Sutton has pointed out, has the ligamentum teres divided into two parts, the upper of which, the cotyloid portion, corresponds to the usual ligamentum teres of mammals; while the lower part, which Chauveau and he term the pubio-femoral portion, passes out through the cotyloid notch and runs forwards and inwards to join the linea alba at its junction with the pubes. It is perhaps doubtful whether it is advisable to speak of this portion of the ligamentum teres as pubio-femoral, because it suggests an identity with the pubo-femoral part of the capsule, a suggestion which, as far as I know, is not intended; probably abdomino-femoral would be a better name. In the ox, sheep, deer, antelope, and chevrotain this abdomino-femoral ligament is not seen, though the rest of the ligamentum teres is well marked. In the goat a large part of the ligament passes out of the cotyloid notch, and is attached to the dorsal part of the capsule after the manner described later in Pedetes. In the rhinoceros, according to Sutton, the ligamentum teres is absent, but I have never had the opportunity of dissecting this animal. In the elephant, specimens in this Museum show that it is wanting in both the

Indian and African species. In Hyrax, Bland Sutton failed to find the ligament, but in my specimen the arrangement was interesting; it was attached by a vertical linear fold to the lower half of the head of the femur; this fold was not entirely free in the joint cavity, but its lower edge was continuous with the lower part of the capsule. When the ligament reached the acetabulum, the greater part of it was continued out through the cotyloid notch, and was attached to the pubes outside the joint; it thus corresponded with the abdomino-femoral band in the horse, and is a point in favour of Bland Sutton's contention that the ligamentum teres is the continuation of some extra-capsular structure. There is a similar specimen in the Museum of this College which shows very much the same arrangement.

In the Rodentia the ligamentum teres is, as far as I know, always present, at least I have found it in a fairly large and representative series of animals.

In the Cape jumping hare (*Pedetes caffer*) it was a somewhat delicate structure, and, as in the goat, horse, and Hyrax, passed out of the joint through the cotyloid notch, but instead of turning ventralwards to the abdomen, or being attached to the pubes, as in the two latter animals, it turned backwards and became continuous with the dorsal part of the capsule, which it tended to tighten in extreme flexion of the joint. The capsule of the hip in this animal suddenly became very thin just before its attachment to the neck of the femur, so that the outer edge of the thick part forms a sphincter round the neck, and it is this sphincter which is drawn tight by the ligamentum teres during extreme flexion. This may possibly be an adaptation to the jumping habits of the animal, but it is certainly another instance of the continuity of the ligamentum teres with extra capsular structures.

It is interesting to notice in this connection that some of the human anatomy text-books remark that fibres of the ligamentum teres are continued out of the hip through the cotyloid notch.

In the Edentata, Bland Sutton found the ligamentum teres absent in the sloth and pangolin. In the latter animal I can confirm his observations from a specimen in this Museum, as well as from a dissection of my own. In both the two-toed (*Choloepus*) and three-toed sloths (*Bradypus*) his experience

agrees with my own, but in the lesser ant-eater (*Tamandua tetradactyla*) the ligament is present and free in the joint, although it consists chiefly of synovial membrane without fibrous tissue. In the armadillo the arrangement of the ligamentum teres was identical with that already recorded in Hyrax, but the lower part of the head of the femur shows a vertical notch as if the sphere was not completed here. This points to the truth of the theory that the ligamentum teres is originally continuous with the capsule, but is cut off by the "confluence of the lateral wings of the caput femoris," as Keith says. It is, at all events,

### b

FIG. 1.—Hip joint of Armadillo (*Dasypus*). *a*, head of femur ;  
*b*, ligamentum teres ; *c*, capsule cut.

quite evident that one must not jump to the conclusion that absence of the ligamentum teres is a characteristic of the Edentata, though when it is present in them, it is usually in a rudimentary condition.

In the Marsupialia the ligamentum teres seems to be constant and well marked. I have found it in the Kangaroos (*Macropus rufus* and *Petrogale xanthopus*), and as far as I could determine, it was put on the stretch during extension of the hip in these animals. It was also seen in the native bear (*Phascolarctus*), the Tasmanian devil (*Dasyurus*), the flying and ground phalangers, and the bandicoot (*Perameles*).

In the Monotremata (*Ornithorhynchus* and *Echidna*) there is no ligamentum teres, nor could I find any trace of such a structure.

*Summary of the Hip Joint.*—The ventral part of the capsule is thickened in man and the anthropoids to form the ilio-femoral ligament; this thickening gradually disappears in the lower monkeys. In the quadrupeds the dorsal part of the capsule is generally the thickest. The ligamentum teres may be entirely

absent, as in the orang, the hedgehog and mole (? other Insectivora), the Pinnipedia, the elephant, sloth, pangolin, and the Monotremata, though I cannot think of anything common to all these animals which could account for its absence, beyond the fact that they are all slow movers. When the ligament is present it may be free in the joint as in most mammals, partially fused with the pubic portion of the capsule, as in the Hyrax and the armadillo, or some of it may be traced to the outer side of the capsule through the cotyloid notch, as in the goat, horse, Hyrax, and Cape jumping hare.

Taking these two latter groups into consideration, the presumption is that the ligamentum teres was originally an extra capsular tendon or other fibrous band which was attached below the head of the femur, and gradually pushed its way into the interior of the joint cavity through the pubic part of the capsule.<sup>1</sup>

#### KNEE JOINT.

In contrasting the anatomy of man's knee with that of other mammals the following points should be kept in mind. In man the external lateral ligament is attached to the head of the fibula, and is a rounded cord; the internal lateral ligament is a flat strap, which is prolonged down the inner side of the tibia for some distance; the posterior ligament is reinforced by oblique fibres from the semi-membranosus muscle; the semilunar cartilages are, as their name implies, both semilunar, and are attached at each end to the head of the tibia, but the external one sends an oblique bundle of fibres up to the femur in close connection with the back of the posterior crucial ligament; the superior tibio-fibular articulation does not, as a rule, communicate with the knee; and the ligamentum mucosum is attached by a delicate fold of synovial membrane to the posterior part of the trochlear surface of the femur, but is not continuous with the synovial membrane lining the crucial ligaments.

In the lower monkeys (rhesus, vervet, baboon, capuchin, and spider monkeys) much more rotation is allowed at the knee than in man, and this is the case during both flexion and extension, consequently smooth cartilage-covered facets are found between

<sup>1</sup> In reference to this, see Sutton on 'Ligaments,' p. 40.



the lateral ligaments and both tuberosities of the tibia, while the internal lateral ligament is not attached to the internal tuberosity and then prolonged down the shaft as in man, but passes straight from the internal condyle downward and forward to the inner surface of the shaft of the tibia.

The lower attachment of the external lateral ligament in the rhesus monkey is to the front of the upper surface of the head of the fibula, but in the spider monkey to the outer side of the neck; it was also noticed that the fibres of this ligament were twisted in such a way that those rising posteriorly from the femur became external and anterior when they reached the fibula. The ligamentum mucosum is continuous with the synovial membrane lining the anterior crucial ligament, so that there is an antero-posterior septum dividing the lower part of the joint into two halves, and making it impossible to pass a probe between the ligamentum mucosum and the anterior crucial ligament, as can so easily be done in man. The posterior ligament of the capsule is not a well-marked structure, and lacks the oblique expansion of the semi-membranosus, which is so characteristic of it in man. The crucial ligaments are not connected, and in *Macacus rhesus* I found that the synovial cavity of the joint was continued between them. The internal semilunar cartilage closely resembles that of man, but the external one, instead of being attached posteriorly just behind the spine of the tibia, is continued obliquely across the back of the posterior crucial ligament to the outer side of the internal condyle of the femur. In man this external cartilage acquires a new attachment behind the spine, but the older one still remains as an oblique band of fibres, closely connected with the back of the posterior crucial ligament, and sometimes spoken of in human anatomy as the ligament of Wrisberg. We shall see later that the simian attachment of this cartilage is the generalised mammalian type, and that man's arrangement is specialised for some purpose, probably as an adaptation to the erect position which results in strong and continual extension of the knee, with great strain on the intra-articular cartilages, especially the outer one, a strain which would possibly result in displacement were it not for the extra security gained by an attachment immediately behind the spine of the tibia. I have

not had the opportunity of dissecting the knee of any of the anthropoids, but I am told by Keith and Duckworth that the arrangement in it more closely resembles that of the lower monkeys than that of man. In the baboon, vervet, and spider monkey the anterior and posterior attachments of the external semilunar cartilage, which otherwise are as in *Macacus*, are connected by a broad band resembling the rest of the cartilage, so that the structure is really circular instead of crescentic. In *Ateles*, too, a fibrous band runs from the anterior part of each semilunar cartilage in such a direction that they both meet in

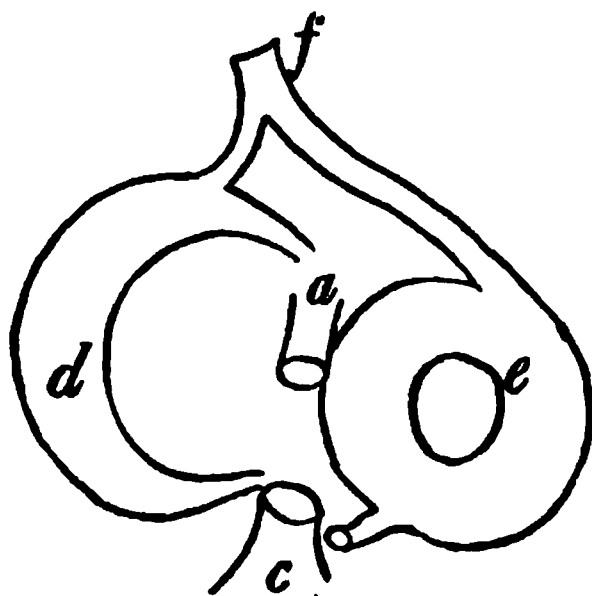


FIG. 2.—Knee joint of Spider Monkey (*Ateles*). *a*, anterior crucial ligament; *c*, posterior crucial ligament; *d*, internal semilunar cartilage; *e*, external semilunar cartilage; *f*, transverse ligament.

front of the internal cartilage, and become merged in the antero-internal part of the capsule. They are less well developed in other monkeys, and I think that the transverse ligament of the human knee must be a remnant of them.

In all the monkeys which I have examined the superior tibio-fibular joint communicated with the knee. In the knee of the lemur the arrangement and attachments of the semilunar cartilages and lateral ligaments closely resembled those of the rhesus monkey already described, but the ligamentum mucosum, instead of being firmly attached to the femur, was not connected with it at all. The chief difference, however, between the knees of monkeys and lemurs lies in the superior tibio-fibular joint. This joint in the lemur allows of free forward and backward gliding movements when the knee is flexed, but not when it is extended. The ligaments attached to the head of the fibula are

four, two superior or external lateral of the knee; also an anterior and a posterior ligament. Of the two superior, which connect the fibula with the femur, the anterior is the usual external lateral ligament; while the posterior, I have little doubt, is the divorced tendon of the popliteus, the fleshy part of which is attached to the tibia and fibula to form part of the tibio-fibularis or rotator fibulæ. The anterior tibio-fibular ligament is a rounded horizontal bundle, considerably longer and

*h* -

FIG. 3.—Knee joint of Lemur from behind. *a*, external condyle; *b*, internal condyle; *c*, external semilunar cartilage; *d*, internal semilunar cartilage; *e*, posterior crucial ligament; *f*, posterior tibio-fibular ligament; *g*, long external lateral ligament; *h*, tendon of popliteus converted into a ligament; *i*, internal lateral ligament.

better defined than in other animals, and at its inner end is attached to the front of the external tuberosity of the tibia. The fourth ligament corresponds to the posterior ligament of the superior tibio-fibular joint in man, but instead of being attached to the tibia it runs upward and inward behind that bone till it reaches the back of the internal semilunar cartilage. During flexion of the knee the fibula is free to glide forward and backward on the outer tuberosity of the tibia, but as soon as the

knee is extended the external lateral ligaments which run downward and backward become tense, and prevent the fibula moving backward; at the same time, during extension of the knee the internal semilunar cartilage becomes longer from before back, and puts the posterior ligament connecting it with the head of the fibula on the stretch, so that the fibula can now move neither forward nor back. I confess that I do not know what advantage the lemur gains from this mobility of the superior tibio-fibular joint, but we shall see a very similar arrangement in many of the arboreal marsupials, and possibly it may be of use in tree-climbing, though why the arboreal monkeys do not possess the same arrangement is difficult to say.

In the Cheiroptera, the fruit bat (*Pteropus*), as I have already pointed out, has the flexor surface of the knee turned forward. No movement except flexion and extension is allowed, and it is interesting to notice that there are no traces of semilunar cartilages, an indication, I think, that these structures are chiefly intended to provide two separate joints, one above for hinge movements, and another below for rotatory or gliding movements. This arrangement reminds us of what we have already met with in the temporo-mandibular joint.

The external lateral ligament, which of course is internal in the bat, is double, and consists of a superficial and a deep part. I have little doubt that, as in the lemur, the deep part is really the tendon of the popliteus which has lost its muscular portion, not, in this instance, because that portion has been separated from it to move the fibula on the tibia, but because, having no rotating work at the knee to do, and no power of moving the head of the fibula, it has disappeared from sheer want of work. The internal lateral ligament is not continued down the shaft of the tibia, and the crucial ligaments show nothing remarkable. The patella is absent, a fact which is probably correlated with the disuse of the limbs as organs of progression. In the long-eared bat (*Plecotus*), which will serve as an example of the insectivorous bats, the knee joint does allow a certain amount of rotation, and in it semilunar cartilages are found as very delicate rings. This bat resembles the fruit bat, however, in the absence of any trace of a patella. In the Insectivora the hedgehog and mole

have typical mammalian knee joints, the external semilunar cartilage is attached to the internal condyle posteriorly, and the crucial ligaments are unconnected; otherwise the joint is as in man. Since the tibia and fibula are firmly synostosed above and below in these animals, there can be no question of the superior tibio-fibular joint communicating with the knee.

The Carnivora, like the Insectivora, in the structure of their knee joint, maintain their reputation for being very generalised mammals, though some little interest attaches to the arrangement of the ligamentum mucosum; sometimes, as in the otter, it may form a vertical antero-posterior septum, reaching from the anterior crucial ligament as high as the lower margin of the trochlea; at other times, as in the bear and hyæna, the ligamentum mucosum is hardly attached to the femur at all.

In the bear (*Ursus Americanus*), the same twisting of the fibres of the external lateral ligament that has already been referred to in the monkey was well seen, and the direction of the twist was the same.

In the Ungulata the semilunar cartilages have the generalised mammalian attachments already described, but the external lateral ligament is modified to suit the disappearing fibula. In the horse, in which the upper part of the fibula is present, the ligament is attached as usual to the head of that bone. In the goat it is attached to the outer tuberosity of the tibia, and afterwards is prolonged down among the muscles as a fibrous cord representing the fibula. In the deer I could find no trace of a fibula, and the ligament ended in the outer tuberosity of the tibia. The characteristic twist of the external lateral ligament was well seen in the deer (*Cervus rufus*) and the antelope (*Tragelaphus scriptus*), and the internal lateral ligament also showed a twist, though not so clearly as the outer. In the internal ligament, the posterior fibres at the femur became internal (superficial) and then anterior at the tibia—that is to say, the ligament was twisted in the opposite direction to the external lateral.

In all the ungulates which I have examined, the ligamentum mucosum has a very extensive attachment to the femur; in the ox it very nearly divides the knee into three joint cavities, one between the trochlea and the patella, and two others between

the condyles and the tibia. In my specimen of the brocket deer (*Cariacus rufus*), the knee was completely divided into two chambers, by a reflexion of synovial membrane, running from the crucial ligaments to the tendon of the extensor longus digitorum, which rises from the outer side of the trochlea; the external condylo-tibial articulation is thus shut off from the rest of the knee joint. In the goat and chevrotain the ligamentum mucosum is well marked, and divides the two condylar parts of the joint from one another, but the trochlear portion communicates with both of them. In the Rodentia the knee joint resembles that of the Carnivora and Insectivora, in being typically mammalian in its arrangements.

In the Edentata, the three-toed sloth (*Bradypus*) has the synovial cavity between the patella and the trochlea completely shut off from that between the condyles and the tibia, and these latter, again, are separated from one another. In the armadillo the separation into three parts was not quite complete, while in the lesser ant-eater (*Tamandua*) and pangolin (*Manis*) the attachment of the ligamentum mucosum to the femur, although broad, does not nearly divide the joint into three. The lower attachments of the lateral ligaments in the armadillo are singularly low, and a great amount of rotation is allowed at the knee joint of this animal.

In the Marsupialia the knee and tibio-fibular joints have several points of interest. The crucial and lateral ligaments, and the semilunar cartilages, have the generalised mammalian attachments—*i.e.*, they are as in man, except that the posterior attachment of the external semilunar cartilage is to the internal condyle. The fibula, as Young has pointed out, is capable of a forward and backward movement at the superior tibio-fibular joint; the forward movement is checked by the external lateral ligament of the knee, while the backward is stopped by the long and strong anterior ligament of the tibio-fibular joint. I have had the opportunity of examining the knees of the following marsupials—Red kangaroo (*Macropus rufus*), Rock kangaroo (*Petrogale*), Wallaby (*Halmaturus*), Phalanger (*Phalangista vulpina*), Flying phalanger (*Acrobates pygmea*), Koala (*Phascolarctus*), Opossum (*Didelphys*), Tasmanian devil (*Dasyurus*), and Bandicoot (*Perameles*), and of these I think the phalanger

showed the greatest specialisation of the joint, while the bandicoot had a much more generalised mammalian knee than the rest. In the koala, the phalanger, the opossum, and the Tasmanian devil, the great mobility of the fibula has produced the same effect on the popliteus that we noticed in the lemur; the fleshy part acquires an attachment to the fibula, while the tendon is converted into an extra external lateral ligament. In all the mar-

FIG. 4.—Knee joint of Opossum (*Didelphys*) from the outer side.  
*a*, external semilunar cartilage in front of twisted external lateral ligament; *b*, in front of anterior tibio-fibular ligament;  
*c*, tendon of popliteus, with sesamoid bone, forming an extra external lateral ligament; *d*, cartilaginous patella.

supials that I have examined, except the bandicoot, the patella is cartilaginous, and consequently these animals must want the leverage which this bone gives in extending the knee. Possibly the absence of a bony patella is made up for by the superior tibio-fibular joint. If the tibia and fibula are forcibly pressed together in the phalanger or the opossum, the head of the fibula will be

seen to glide forward and inward, and, as the condyle of the femur is in contact with it during flexion of the joint, this forward and inward movement causes the knee joint to extend with considerable force; the extension of the knee thus started, is carried on by the external lateral ligament dragging the femur above its axis of rotation after the advancing head of the fibula. A circumstance which confirms me in the opinion that the leverage which the quadriceps extensor loses through the absence of the patella is made up for by the tibio-fibular muscle moving the fibula, is that in the bandicoot (*Perameles*) the tibio-fibular joint allows very little movement, the fibula never articulates with the femur, and the popliteus tendon, instead of being converted into an extra external lateral ligament, is continuous with its fleshy belly as usual. In this animal, therefore, the fibula can have little or no action in extending the knee, and we find that the patella, instead of being a pad of cartilage, as in other marsupials, is an elongated bone, as in most other mammals. It must not be imagined, however, that the loss of the patella is always compensated for by the mechanism I have described, for, in the kangaroos and wallabys, nothing of the kind exists; the fibula never touches the femur, and is not capable of great approximation to the tibia, nor does it in any way assist in the extension of the knee; in spite of this the patella is as distinctly cartilaginous as in the opossum or phalanger.

One ought not to leave the knee joint of the marsupials without noticing the great size which the external 'fabella' attains.

In the Monotremata, the *Ornithorhynchus* resembles the sloth in having the knee completely divided into three compartments by the ligamentum mucosum.

Both the external, and, as far as I could see, the internal semilunar cartilages, are attached to the femur posteriorly. The fibula articulates with the external condyle of the femur as well as with the tibia. The patella, unlike that of the marsupials, is large and is connected with the top of the fibula by a transverse ligament. The knee of the *Echidna* resembles that of *Ornithorhynchus*, except that the division of the joint into three is not quite complete. The anterior crucial ligament is divided into two bundles, which lie side by side, and the posterior horn of the internal semilunar cartilage turns up with the outer of these,



and so is attached to the femur. The external semilunar is attached to the femur posteriorly, as in other mammals. The

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FIG. 5.—Knee joint of *Ornithorhynchus* from outer side. *a*, fibulopatellar ligament; *b*, on fibula below external lateral ligament; *c*, ligamentum patellæ.

patella is very broad. The superior tibio-fibular joint communicates with the knee, and when the tibia and fibula are approxi-

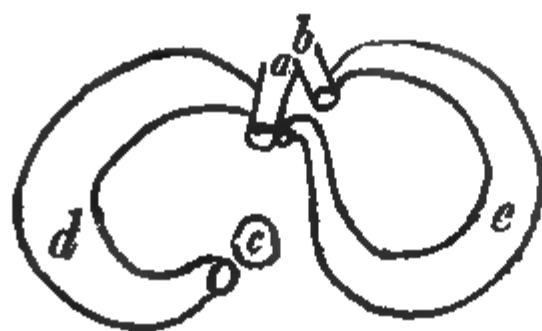


FIG. 6.—Knee joint of *Echidna*. *a* and *b*, double anterior crucial ligament; *c*, posterior crucial ligament; *d*, external semilunar cartilage; *e*, internal semilunar cartilage.

mated, the head of the latter glides forwards, as it does in marsupials.

*Summary of the Knee.*—The external lateral ligament of the knee in all mammals (including man) is twisted in such a way that the fibres attached posteriorly to the femur become external,

and then anterior when they reach the tibia. In some mammals a twist in the opposite direction is found in the internal lateral ligament. The ligamentum mucosum may be (1) quite unconnected with the femur as in the lemur; (2) slightly connected with it as in man; (3) forming an antero-posterior partition between the two condylar joints, as in most monkeys and the otter; (4) completely separating the knee into three cavities, two condylar and one trochlear, as in the three-toed sloth and duck mole; (5) separating the joint into two unequal parts, one trochleo-condylar and the other condylar, as in the brocket deer. The most primitive arrangement of the semilunar cartilages seems to be that both are attached posteriorly to the tibia, as in the duck mole and spiny ant-eater (*Ornithorhynchus* and *Echidna*). In man both horns of both semilunar cartilages are attached to the tibia. In other mammals an intermediate arrangement exists, and the external cartilage is attached posteriorly to the femur, the internal to the tibia. In the fruit bat, where no rotation of the knee occurs, there are no semilunar cartilages. In most monkeys the external semilunar cartilage forms a complete circle.

In certain marsupials the patella is cartilaginous, and this is coincident with a peculiar mobility of the superior tibio-fibular joint by which extension of the knee is assisted. In most mammals the superior tibio-fibular joint, when it is present, is continuous with the knee joint. Man is an exception to this.

#### THE ANKLE JOINT.

In contrasting the ankle joint of monkeys with that of man one is struck by the feeble development of the anterior fasciculus of the external lateral ligament. Keith has already pointed this out, and I am able to state that in my specimens of vervet and baboon the bundle was entirely absent, while in the macaque it was so feeble as to require careful looking for. This ligament in man checks lateral movement of the joint, and is most tense when the foot is at a right angle with the leg. I have had no opportunity of studying it in the anthropoid apes, but as far as my researches go, it is limited to certain monkeys and man, and therefore its presence is presumably

connected with the maintenance of the erect position. In the spider monkey and lemur the middle fasciculus of the ligament is found attached to the anterior border of the external malleolus instead of to the tip of that process. The internal lateral ligament in all the monkeys I have examined (baboon, three macaques, vervet, capuchin, and spider monkey) is distinctly divided into an anterior and posterior band; of these the anterior consists of a superficial and deep portion. The superficial runs to the navicular bone, and then on to the metatarsus; it is described by Keith as the internal tibio-tarso-metatarsal liga-

FIG. 7.—Ankle joint of Vervet Monkey (*Cercopithecus*) from inner side. *a*, tibia above epiphysial line; *b*, astragalus behind posterior fasciculus of internal lateral ligament; *c*, astragalus in front of anterior fasciculus of interior lateral ligament; *d*, sustentaculum tali; *e*, navicular; *f*, internal cuneiform; *g*, middle cuneiform; *h*, first metatarsal.

ment, while the deep part runs to the navicular bone and calcaneo-navicular ligament. The posterior part of the internal lateral ligament is not so strong, and runs downward and backward to the posterior part of the internal surface of the astragalus; it is broad and quadrilateral. The articular surface of the lower end of the monkey's tibia differs from that of man, in that it extends somewhat on to the front of the bone and comes into contact with the neck of the astragalus during dorsal flexion of the ankle; this arrangement has been noticed in some of the lower races of man. The inferior tibio-fibular joint of monkeys differs little from that of man, except that there is rather more synovial membrane.

In the lemur the ankle joint is practically identical with that of the monkeys, and there is no anterior fasciculus of the external lateral ligament; there is a good deal more movement, however, in the inferior tibio-fibular joint.

In the Cheiroptera the fruit bat (*Pteropus*) has the lower end of the fibula ending in a flat articular surface, which plays on a corresponding surface on the calcaneum. The joint between these two is completely shut off from the rest of the ankle joint, and there is a very definite extension of the synovial membrane of the ankle between the lower ends of the tibia and fibula.

In the Insectivora the hedgehog, mole, and shrew have the tibia and fibula fused together in the lower part of the leg. The external malleolus articulates by its tip with the calcaneum during dorsal flexion. As in all mammals below the higher Primates, the anterior fasciculus of the external lateral ligament is absent, and the middle fasciculus is attached to the front of the malleolus, and is nearly horizontal in direction. The posterior fasciculus is distinct, and connects the fibula with the astragalus as usual.

The internal lateral ligament is now seen in its generalised form; it consists of two definite bands—the anterior and more superficial passes to the navicular bone (tibio-navicular), while the posterior and deeper one is tibio-astragalar.

In the Carnivora the fibula is always distinct from the tibia at its lower end, and only the middle and posterior fasciculi of the external lateral ligament are present. Unlike the Cheiroptera and Insectivora, the fibula does not directly articulate with the calcaneum. In the Ungulata special arrangements are adopted to make the ankle a perfect hinge. In addition to the exact fitting of the lower end of the tibia into the deep trochlea of the astragalus the external lateral ligament is X-shaped, and so is tight in all positions of the joint. The deep portion of the X runs downward and backward, and is no doubt the middle fasciculus of the external lateral ligament of human anatomy, but the superficial limb which runs downward and forward has no representative in the more generalised ankles hitherto described. The anterior margin of the articular surface of the tibia is bevelled in most Artiodactyla; when the foot is dorsally flexed for rather over a right angle this margin comes

in contact with the front of the facet on the astragalus, and movement of the ankle joint is brought to a standstill. It must not be imagined, however, that the foot cannot be dorsally flexed further than this, for the head of the astragalus continues the hinge movement, and rotates round a transverse axis until the astragalus is at right angles with the long axis of the foot. In this way dorsal flexion can be carried on until the metatarsals are nearly parallel with the tibia. The hinge-like steadiness of the ankle is increased by the external malleolus being concave from before back at its lower end, and articulating with a similar

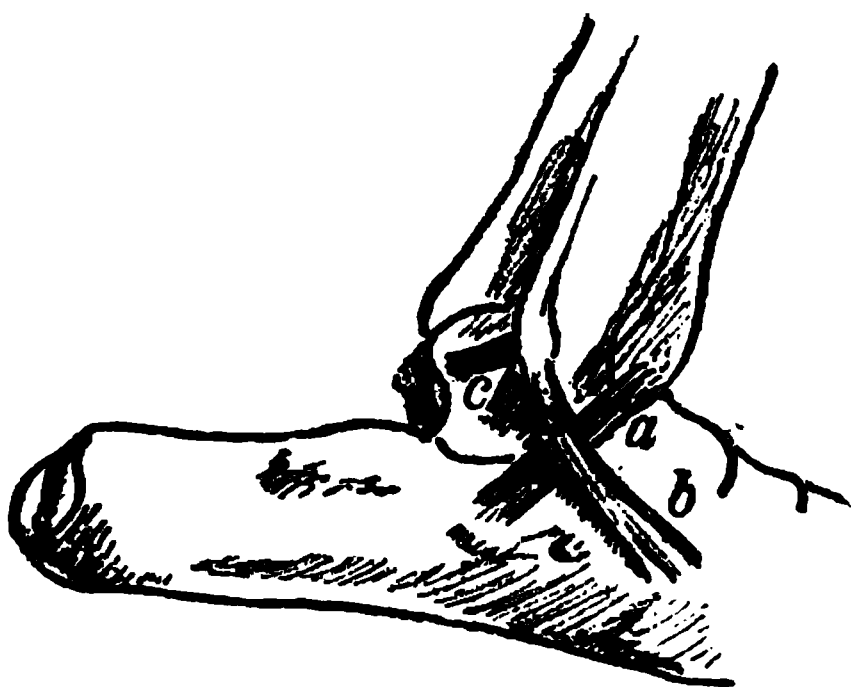


FIG. 8.—Ankle joint of Chevrotain (*Tragulus*) from outer side.  
*a*, middle fasciculus of external lateral ligament; *b*, extra ligament forming an X; *c*, posterior fasciculus.

convexity on the calcaneum. The internal lateral ligament consists of the two usual parts, the tibio-navicular, which is very strong, is superficial to and almost covers the tibio-astragalar portion; in addition to these there is another and more superficial band, which runs downward and backward across the tibio-navicular portion, and so forms an X on the inner side of the joint. The above description of the ligaments, which is taken from an examination of the ankle of the deer, antelope, and goat, seems to hold good for most ungulates; the bony surfaces are, however, liable to vary with the presence or absence of the lower end of the fibula. Hyrax is remarkable for the way in which the internal malleolus forms a spherical knob, which projects into a concavity on the inner side of the astragalus.

In the Rodentia the ankle is fairly generalised, the antero-posterior notch in the trochlear surface of the astragalus is very deep, and dorsal flexion of the ankle is stopped by the tibia and astragalus coming into contact anteriorly. The two bands of the internal lateral ligament are distinct, but the anterior one is sometimes, as in the case of *Pedetes*, attached to the sustentaculum tali instead of to the navicular. In the external lateral ligament of *Pedetes* and *Dipus* the same arrangement for forming an X ligament, already noticed in the Ungulata, is found. The external malleolus does not articulate with the calcaneum.

In the Edentata most of the species, such as *Dasypus*, *Manis*, and *Tamandua*, have a very generalised ankle, agreeing with that already described in the Carnivora and Insectivora. In *Bradypus*, however, the external malleolus forms a convex pivot, which fits into a concavity on the outer side of the astragalus, an arrangement resembling that of *Hyrax*, but on the opposite side of the joint.

The Marsupialia are remarkable for the possession of a structure which is not found in the ankles of other mammals. My attention was first called to it by Mr Pearson, the Professor of this College, in the Tasmanian devil. In this animal it closely resembles the semilunar cartilages of the knee, and lies between the lower end of the fibula and the astragalus. The two horns of the semilune are directed outwards, the posterior being attached to the fibula just behind the external lateral ligament, while the anterior one is attached to the calcaneum in front of the lower attachment of the same ligament. This structure is present in all the marsupials which I have examined, but is best seen in those in which the fibula is very movable, such as the Tasmanian devil, phalanger, and opossum. In the kangaroo it is present, but does not form a semilune; instead it runs obliquely downward and forward on the inner side of the external lateral ligament. I think that its attachments and its arrangement in the kangaroo point to its being derived from some of the inner fibres of the so-called middle fasciculus of the external lateral ligament, and its presence is possibly explained by the fact that in most marsupials there is a certain amount of rotation of the fibula on its long axis in addition to the ordinary hinge movement of the

ankle. What I have seen of complete and partial menisci in joints makes me think that their presence generally indicates two or more different kinds of movement, and that their origin is more likely to be an ingrowth from the surrounding capsule than a modification of some ancestral structure. In the kangaroos the same X-like arrangement of the external lateral ligament seen in Ungulates and *Pedetes* is found.

In the Monotremata both *Ornithorhynchus* and *Echidna* have the internal malleolus knobbed, as in *Hyrax*, to fit into the inner side of the astragalus, and so form a pivot. The external lateral ligament consists of only one very strong fasciculus, but

FIG. 9.—Ankle joint of Wallaby (*Halmaturus*) from outer side.  
*a*, mid fasciculus of external lateral ligament; *b*, extra fasciculus; *c*, posterior fasciculus; *d*, rudimentary interarticular meniscus; *e*, calcaneum; *f*, fibula; *g*, tibia; *h*, cuboid.

instead of being attached to the fibula it comes from the anterior margin of the lower end of the tibia close to the fibular articulation. It runs downward and backward to the calcaneum, and is evidently the middle fasciculus of the external lateral ligament of human anatomy. Its attachments and direction forcibly remind one of the arrangement of the fibres in the dorsal ligament of the carpus, which runs obliquely from the radius to the cuneiform in man and most other mammals.

*Summary.*—The anterior fasciculus of the external lateral ligament disappears in the lower Primates, and is probably

an adaptation to the erect position. When the anterior fasciculus has disappeared the middle one occupies its point of attachment to the front of the external malleolus, but in the monotremes it is fixed to the front of the tibia; there is therefore some reason to think that the middle fasciculus of the

FIG. 10.—Ankle joint of *Phalanger* from outer side. (The fibula has been removed.) *a*, tibia; *b*, head of astragalus; *c*, interarticular meniscus; *d*, ossification in meniscus; *e*, posterior fasciculus of external lateral ligament; *f*, middle fasciculus of external lateral ligament; *g*, calcaneum, *h*, cuboid.

external lateral ligament of the ankle is serially homologous with the dorsal ligament of the wrist joint, while the posterior fasciculus would probably be the serial homologue of the ulno-carpal band of the palmar ligament of the wrist, and the tibio-astragalar bundle of the internal lateral ligament of the ankle the serial homologue of the radio-carpal part of the palmar ligament of the wrist. This would leave the tibio-navicular bundle of the internal lateral ligament of the ankle as the serial homologue of the external lateral or radio-scaphoid ligament of the wrist.



Special protection against lateral movement of the ankle is attained in animals with a long foot, such as the ungulates, the kangaroo, and the Cape jumping hare, by additional lateral ligaments, which cross the permanent ones in such a way as to form an X.

In many marsupials a semilunar fibro-cartilage is interposed between the fibula and astragalus, and there are reasons for believing that this is derived from some of the fibres of the external lateral ligament. In these animals rotation as well as gliding and hinge movements take place at this joint, and this is one of the instances which make me believe that intra-articular menisci are formed in those joints where more than one kind of movement is present, and that, as in the bat's knee, they tend to disappear when only one kind of movement persists.

## ON A MODIFICATION OF THE HELMHOLTZ THEORY OF HEARING.<sup>1</sup> By ALBERT A. GRAY, M.D., F.R.S.E.

WHEN engaged in examining, under the microscope, a section of the cochlea of the white mouse, the writer was struck by an anatomical fact which appeared to him to be of considerable importance in regard to the question as to the way in which this organ performs its function.

The fact referred to is simply this, that the ligamentum spirale increases in size and becomes more distinctly fibrous as it passes from the apex of the cochlea to the base. The transition, though gradual, is a very pronounced one in both respects, and it is to be added that the larger and more fibrous it becomes, it takes up the usual microscopic stains, particularly the extra nuclear ones, with increasing avidity. The accompanying figure shows these facts plainly enough. It represents a section of the human cochlea.

On observing this fact, sections of the cochlea of other animals were examined, and the same fact was found to be true in all cases. The animals were the guinea-pig, rat, rabbit, kitten, calf, and the human subject, and in the last it was most pronounced. We may therefore assume that it is true of all mammals.

Now whether this has been described by anatomists before or not, it has not had that attention at the hands of the physiologist which it deserves, for if we take it in relationship to the other well-known facts concerning the basilar membrane and its appendages, it is remarkable. Thus it is well known, and has often been cited in physiological discussions, that the basilar membrane itself gradually diminishes in breadth from apex to base, while the rods of Corti, the hair-cells, and the hairs themselves, all become smaller.

It was this diminution in size of the structures connected with Corti's organ which Helmholtz urged strongly in support of

<sup>1</sup> Read at a meeting of the British Association for the Advancement of Science, held at Dover, September 1899.

his well-known theory that the analysis of sound takes place in the cochlea. He looked upon the basilar membrane as being made up of many strings, those at the apex being comparatively long, while those at the base were short; the former, therefore, were supposed to resonate in sympathy with deep notes, and the further down the basilar membrane we go, the shorter do the strings become, and, therefore, resonate in sympathy with higher notes. Each string, therefore, according to Helmholtz, vibrates




FIG. 1.—In preparing the section of which this is a photograph, the lowest portion of the basilar membrane became dislocated upwards and laterally; hence it appears twice in the lowest whorl to the left.

in sympathy with a particular note. Keeping this in view, it will be of interest to see how the fact above referred to affects the correctness of this theory.

In the first place, it is clear that since the *ligamentum spirale* consists either of unstriped muscular fibre, or, more probably, of fibrous connective tissue, it must produce tension on the basilar membrane. And further, since, as above described, it increases greatly in size from the apex of the cochlea to the base, then the tension exerted by it on the basilar membrane must increase to

a corresponding extent. Now, if we look upon the basilar membrane as a series of strings, as Helmholtz did, then these strings must be under gradually increasing tension the further towards the base of the cochlea we go, and this being so, their vibration-frequency must increase correspondingly. The fact of the increasing size and strength of the ligamentum spirale downward, therefore, strengthens immensely the view that sound is analysed into its simple harmonic constituents by the cochlea. The change in size of the structures of the organ of Corti, and the diminution in breadth of the basilar membrane, might be mere coincidences, or might not alone be sufficient grounds for supporting this view, but when we have associated with these the remaining factor, tension, which would affect the pitch of the membrane, then the evidence appears overwhelming.

It must be noted that we are not as yet dealing with the exact way in which the cochlea may analyse sound, but only with the question as to whether it analyses sound at all, as Helmholtz maintained, or not, as Voltolini, Rutherford, and Waller held. This fact of the increasing size of the ligamentum spirale downward, which has not claimed the attention of physiologists, appears to the writer to be exceedingly strong evidence in favour of the view that sound is analysed in the cochlea so far as it is ever analysed at all.

The anatomical facts in favour of the view that sound is analysed in the cochlea are thus so strong, that it seems almost a work of supererogation to add other objections to the telephone theory, as it has been called, of Rutherford and Voltolini. This theory, shortly stated, is, that the basilar membrane vibrates as a whole to every note, and the nerve fibres transmit to the brain stimuli of a frequency the same as the vibrations of the notes.

In addition to the well-known objections to this theory, the present writer has to add another, which is founded upon pathological evidence. He had the opportunity of seeing a post-mortem examination upon the body of a young man whom he had examined during life for deafness and loud singing noises in the ear. At the post-mortem no disease of either the middle ear or labyrinth was found, but in the substance of the medulla, and involving the roots of the auditory nerve, was a small tumour. One or two other cases of a similar description have been re-

corded (Siebenmann, "Ueber d. central. Hörbahn," etc., *Zeitsch. f. Ohrenh.* Bd. xxix., s. 78).

Now it is surely impossible to conceive of a slowly-growing tumour stimulating the nerve fibres at a given rate per second, and yet if the telephone-theory were correct, it would require such a condition of affairs to produce the sensation of a singing noise. On the other hand, such a case offers no objection to the view that sound is analysed in the cochlea, for these theories only require that if the nerve fibres be stimulated in any way the sensation of sound will be produced in the mind.

There are other objections to the telephone-theory of the cochlea, but they have been published elsewhere. (Vide *Text-book of Physiology*, vol. ii., edited by Schäfer. Chapter on "Hearing," by M'Kendrick and Gray. In course of publication.)

It only remains to add that an objection to the view that sound is analysed in the cochlea, has been made in reference to the differential tones. These tones, according to those who put forward this objection, cannot set resonators in vibration, and must therefore be generated in the mind of the listener, which, if it were true, would be fatal to the theory that sound is analysed in the cochlea by sympathetic resonance. Recent investigation, however, by Forsyth and Sowter (*Proc. Roy. Soc. Lond.*, lxxxiii., 1898, p. 396), has shown that differential tones can be resonated if the resonator is sufficiently accurate. Furthermore, it has been pointed out that differential tones may be generated in the middle ear—Helmholtz (*Tonempfindung*, 3rd edit., trans. by Ellis, p. 237), Preyer (Wiedemann's *Annal.*, xxxviii., s. 131), and others; and this would fully account for the fact that it is admittedly difficult, though not impossible, to resonate differential tones.

There is, therefore, no satisfactory objection to the view that sound is analysed in the cochlea, and we have seen that both on anatomical and pathological grounds there is very good evidence in favour of this view. Other reasons in support of it will be found in Schäfer's *Text-book of Physiology*, vol. ii., *loc. cit.*

Having thus cleared the ground, we may now go on to discuss the means by which sound is analysed in the cochlea.

The first subject that comes under notice is the theory of Helmholtz. This theory is very simple, and is well known.

Helmholtz looked upon each transverse fibre of the basilar membrane to be tuned to a particular tone and no other, so that when that tone, either by itself or in conjunction with other tones, is transmitted to the fluid in the labyrinth, the fibre (possibly also one or two adjacent ones) is set in sympathetic vibration. The nerve-fibre which is in contact with the hair-cell corresponding to that fibre, will thus be stimulated, and, the stimulus being carried to the brain, we are conscious of the existence of that particular tone. When the tone is a compound one, therefore, those fibres of the basilar membrane which are in sympathy with the several simple tones of which the compound tone is composed, will be set in vibration, and we become conscious of the co-existence of several simple tones of different pitch.

This theory in some respects suits the facts of the case very well. It is in keeping with the gradual decrease which the fibres of the basilar membrane undergo in length from apex to base. It is, further, in keeping with the increase in size and strength of the ligamentum spirale downwards, as described at the beginning of this paper, though unknown when Helmholtz put forth his theory. For obviously, as the fibres become shortened and more tense towards the base of the cochlea, their vibration-frequency becomes increased. Helmholtz's theory also explains the fact, which has been discovered by pathological and clinical examination, that when the lower turns of the cochlea are affected by disease the hearing for the higher musical notes is lost.

To the acceptance of Helmholtz's theory as it stands there appears to the writer to be some very serious objections; indeed, unless they are explained these are fatal to the theory. Amongst other objections which have occurred to the writer are these:—The existence of noise as distinguished from musical sounds; the fact that the ear is, under certain circumstances, able to appreciate difference of phase.

Helmholtz appears to have been, to a certain extent at least, aware of these difficulties, for he tried to explain the first in a way which we now know to be inadmissible, and he denied the truth of the second altogether, whereas we know now that the ear does appreciate phase under certain circumstances.

Taking up the first difficulty, the existence of noise as distinguished from musical sounds.

Helmholtz first of all makes the assumption that a sound is noisy in character on account of the irregularity of the wave. But upon examination this assumption is found not to be warranted, as the writer has found out by the following experiment.

Four tuning-forks (two  $ut_4$ ,  $si_3$ , and  $si_{3b}$ ) were taken; these forks were weighted so as to form a series, with intervals of about twelve to twenty vibrations per second, so that when any two consecutive forks were sounded they gave twelve to twenty beats per second. When all were sounded together with the requisite intensity a *noise* was produced, with only a very slight trace of musical element in it. In this case, of course, the wave form would be very irregular. The next step was to take four forks each one octave above the other, and mistune them in the same way as the first set were mistuned. The forks selected were:— $ut_2$  (128 v.d.),  $ut_3$  (256 v.d.),  $ut_4$  (572 v.d.),  $ut_5$  (1024 v.d.), and each was mistuned so as to give approximately twelve beats with the preceding one; thus the second fork gave twelve beats with the first, the third gave twelve beats with the second, and the fourth gave twelve beats with the third. When these were all bowed together the resulting sound was not merely a noise, but a musical sound, though, of course, a somewhat discordant one. There was a slight noisy element present, but this was probably due to the upper partials of one fork having a pitch nearly the same as the upper partials of some of the others, and thus producing a noise in exactly the same way as in the preceding experiment. Experiments of this kind with tuning-forks are, of course, rough, on account of the difficulty of getting the requisite intensities and also of getting the proper intervals. A series of suitable organ pipes would, no doubt, give more satisfactory results.

Now, in the second experiment, the vibrations or the wave-forms representing them are just as irregular as in the first one; in fact, they are probably more so, but the resulting sound was much more musical in the second experiment. It appears, therefore, that the noisy character of a sound does not depend only upon irregularity of vibrations, as Helmholtz assumed.

To proceed further. After assuming that noise was due to

irregularity of the vibrations, Helmholtz suggested that the portions of the labyrinth which were concerned in transforming these vibrations into nerve-stimuli were the *crista* and *macula acustica*. At the time Helmholtz wrote, the suggestion, although a matter of conjecture, was perfectly legitimate, but in the light of subsequent research by Crum Brown, Mach, Goltz, Ewald, and many others, physiologists have come to the almost unanimous opinion that these structures are not concerned in the perception of sound.

We are therefore driven to the conclusion that noises as well as musical sounds are perceived by means of the cochlea.

There is yet another objection to Helmholtz's theory. Noise has pitch. It is not meant that the exact pitch, in the musical sense of the term, can be given, but it is a matter of common observation that noises have pitch relative to one another. Thus, the ticks of different watches have different pitches. Irregular shaped blocks of wood or iron, or indeed any substance, give noises of different pitch according to their size, shape, and texture, although the sounds given forth are clearly noises and not musical sounds. If, then, the cochlea enables us to judge of the pitch of a musical sound, it is but reasonable to suppose that it also enables us, though more roughly, to judge the pitch of a noise, especially when we remember that there is no sharp line of division between noises and musical sounds.

Further evidence of the relationship between noise and pitch is furnished by the following experiment. A set of four forks at close intervals were taken and mistuned, as in the previous experiment, so that the second gave about twelve beats with the first, the third gave about twelve beats with the second, and the fourth gave about twelve beats with the third. Then another set of higher forks, also at close intervals, were mistuned in exactly the same way. When all the first set of forks were bowed a noise resulted with hardly any musical element in it. So also when the second set were bowed the result was only a noise. But in the second case the noise was clearly of a higher pitch than the first.

From these experiments the natural deduction is that noises have pitch relative to one another, and that the sound vibrations affect the nerve-terminations in the cochlea in some way unex-



plained by the theory of Helmholtz. For if the noise were analysed into its constituents by the transverse fibres of the basilar membrane, why is it that we can obtain little or no musical element from the sound however much we concentrate our attention, and still less can we analyse the sound? In this respect noise differs from a discord. A discord may be, and often is, clearly a musical sound.

As regards the perception of the difference of phase of a sound by the ear the question is a somewhat complicated one.

Of course the single ear<sup>1</sup> can distinguish no difference between the two phases of a pure simple tone. Neither can the ear distinguish the difference in phase in a complete harmony, and from experiments which I have carried out I find that the single ear perceives no difference in phase in a mistuned unison. But Lord Kelvin (*Proc. Roy. Soc. Edin.*, vol. ix. p. 602) showed that in the case of imperfect harmonies other than a unison, the ear did notice a difference according to the phase. The difference was for the most part more noticeable in imperfect ternaries than binaries.

Helmholtz's explanation of this is that the ear does not perceive a difference in the phase, but that some upper partials of the two notes were beating together. To this, however, there is the objection that the sounds were produced by tuning-forks, the purest of all tones.

There is yet one other objection which the writer would like to make against the theory of Helmholtz, and which he deduces from the following experiment:—Two *ut*<sub>3</sub> tuning-forks were chosen, and one was mistuned to give four beats per second with the other. When the forks were sounded separately the difference in pitch was clearly noticeable. On sounding the two together the beats were of course heard, but there was no analysis of the sound into its two constituents. That is to say, there was heard only one note, subjected of course to the interruptions of the silences.

Now, if the ear really analysed the sound then we should have been able to distinguish the difference in pitch of the two

<sup>1</sup> The power of the two ears, separately, to perceive differences of phase as described by Prof. S. P. Thompson, does not come into consideration in this matter.

generating notes even better than when they are sounded separately, for we should have the opportunity of simultaneous comparison as in the case of two approximate shades of colour seen by the eye. Of course the difficulty cannot depend upon the want of delicacy of the ear, because, as we saw, it can perceive the difference clearly enough if the forks are sounded separately. If, however, beats are produced on an imperfect harmony other than a unison, then the beats are heard, and the difference of pitch of the two generating notes is also perceived clearly enough.

In view of these difficulties in the way of accepting Helmholtz's theory as it stands, the writer ventures to put forward the following modification of that theory.

Suppose the basilar membrane to be uncoiled and looked at from above, as in fig. 2, then since it is tense in its transverse and not in its longitudinal direction, we may look upon it as a series of minute strips of membrane, or, as Helmholtz considers, of strings, running from the tip of the osseous spiral lamina to the ligamentum spirale. And each of these strips may have a vibration-frequency such that it is set in sympathetic vibration by sound vibrations of exactly the same frequency.

Suppose a note is sounded of a frequency exactly as that of the strip at AA (fig. 2, p. 335), then that strip or fibre will vibrate with a considerable amplitude, and the nerve in connection with the hair-cells at A will be stimulated. Now Helmholtz considered that this (or at most two or three fibres) was all the portion of the membrane that would vibrate, and Rutherford made the well-founded objection that the fibre could not vibrate alone, but would drag the portion of the membrane on each side along with it. If this were the case, then, when a pure tone was sounded, we should hear that tone strongly, and a few higher and lower in pitch along with it more feebly.

It appears to the writer that if the fibre at AA has a vibration-frequency exactly the same as the note sounded then, it will vibrate with a certain amplitude. But since the fibre at BB is only a very minute amount longer, and subject to a tension only a minute degree less than AA, it also will vibrate in sympathy with the note, though not with quite so great an amplitude. Similarly the fibre at DD will vibrate in sympathy

with the same note, but with an amplitude less than BB, and so on, until at, say, EE, the amplitude of movement of the fibre will be so small as to be negligible.

In the same way, if we proceed down the basilar membrane, the fibre CC, being a minute amount shorter, and subject to tension a minute amount greater than AA, will vibrate in sympathy with the note, but with an amplitude less than AA. So also the fibre at GG will vibrate in sympathy with the note, but with less amplitude than CC, and so on until at FF the vibrations are so small as to be negligible.

It must be added that this is not a matter of conjecture, but is strictly in accord with the laws of sympathetic resonance.

Suppose now that we make a longitudinal section through the basilar membrane when the same note was being sounded, we should find that, at the end of one phase of the wave, it was

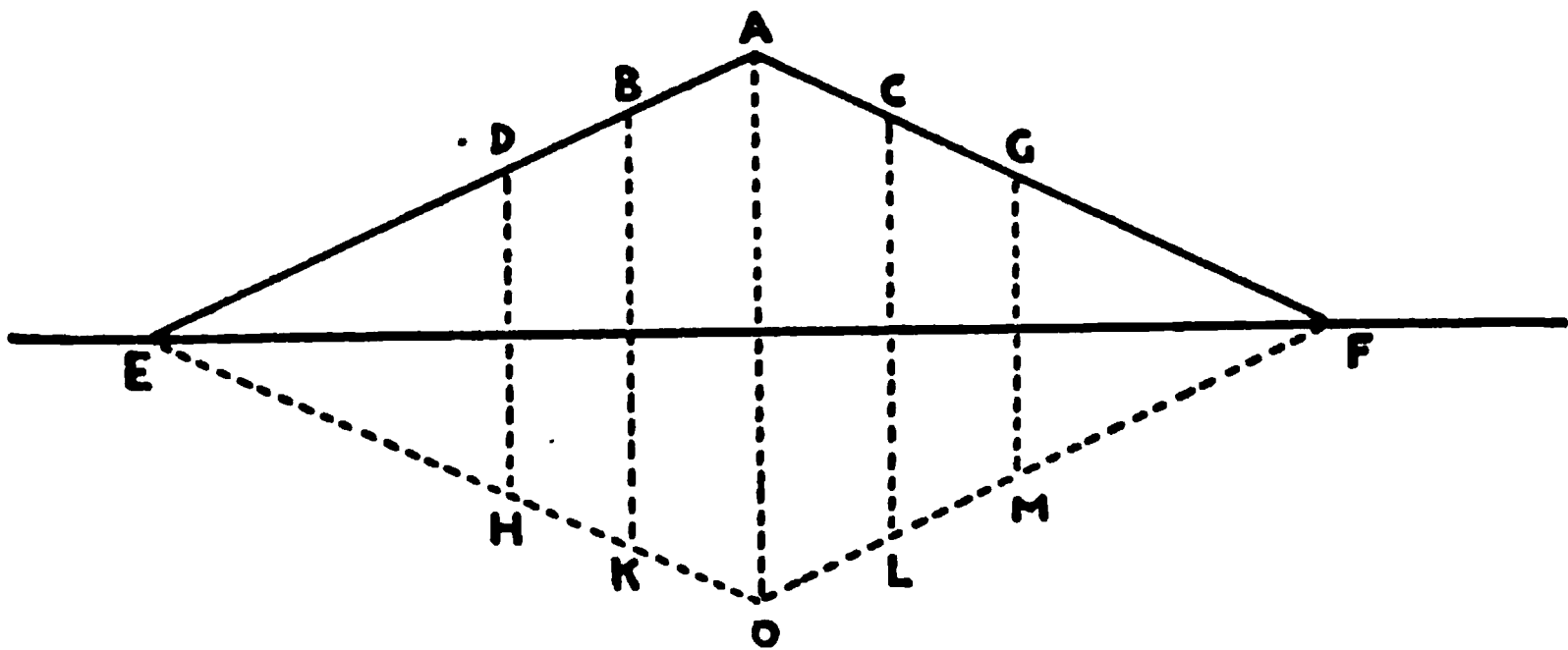


FIG. 3.

raised from its position of rest and had become bent, the bend being of course at the point where the fibre AA was cut transversely, as in fig. 3. At the end of the opposite phase of the wave the bend would occur at a point exactly opposite.

The whole amplitude of the movement of the fibre A would therefore be represented by the line AO, that of the fibre B by the line BK, and so on, until at the points E and F the fibres, having a vibration-frequency so far removed from the note, would move to an extent so small as to be negligible.

When the fibres move as described, then the hair-cells attached to their inner extremities would be carried along with them; so that in the movement upwards the hairs of the hair-cells

would be pressed against the tectorial membrane, and the pressure would necessarily be communicated to the nerve-fibre or fibres terminating at the base of the hair-cells. Hence the nerve-fibre at A would receive the greatest pressure, those at B and C would receive less than that at A, but more than those at D and G, and so on.

Now the question arises, Why is the listener conscious of only one note when, according to the supposition based on perfectly correct acoustical grounds, many nerve-terminations are stimulated? That is to say, why do we not hear more feebly several notes a little lower in pitch than the one sounded, and also some a little higher in pitch?

This is a purely physiological question, and we can get evidence on the subject from another sense very closely allied to that of hearing. I refer to the sense of touch. In both these senses the nerve-terminations are stimulated by mechanical pressure, whereas the other three organs of special sense are probably stimulated by chemical changes. In the following pages it will be shown still further that the sense of hearing is only an exquisitely delicate sense of touch; but at present the fact that both the sensations of hearing and of touch are due to stimulation of the nerve-terminations by mechanical pressure, is sufficient to point out in which direction to look for an analogy.

If we take a pointed instrument, not so sharp, however, as to pierce the skin, and press it very gently against the tip of the finger, we are conscious of pressure at a point. If we press it harder the sensation of a pressure at a point remains, and we may press it so firmly as to render the tissues anæmic for an area of a centimetre in diameter, but still the sensation of pressure at a point remains. Now in this case many nerve-terminations have been stimulated, and that strongly, yet we are quite unconscious of the fact. In other words, although many nerve-terminations have been stimulated, the mind pays no attention to these, but is only conscious of stimulation of that fibre or those fibres which have undergone a maximum degree of stimulation. This is the important point to be kept in mind, and that upon which the whole of the writer's hypothesis depends; but it must be explained that the word maximum is used in its mathematical sense; that is, if immediately on each side of a

point of pressure there are other parts which are undergoing less pressure, that point is termed a maximum point, even

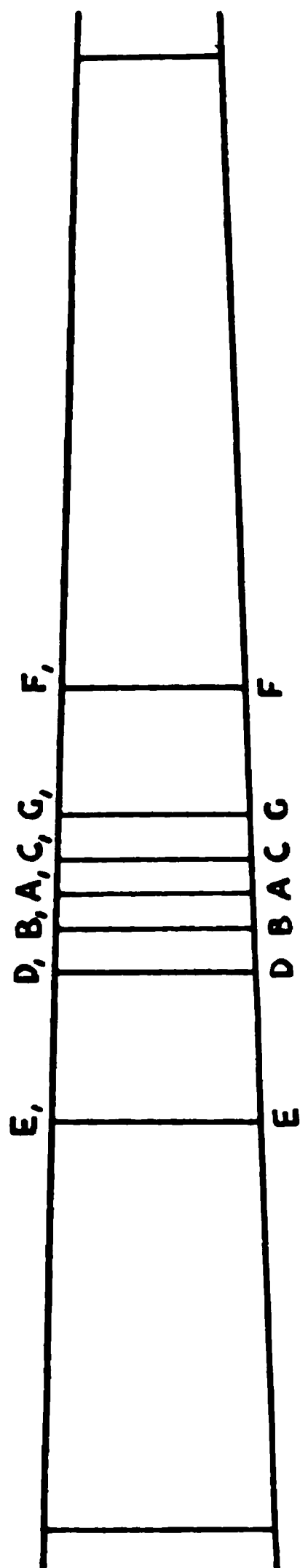


FIG. 2.

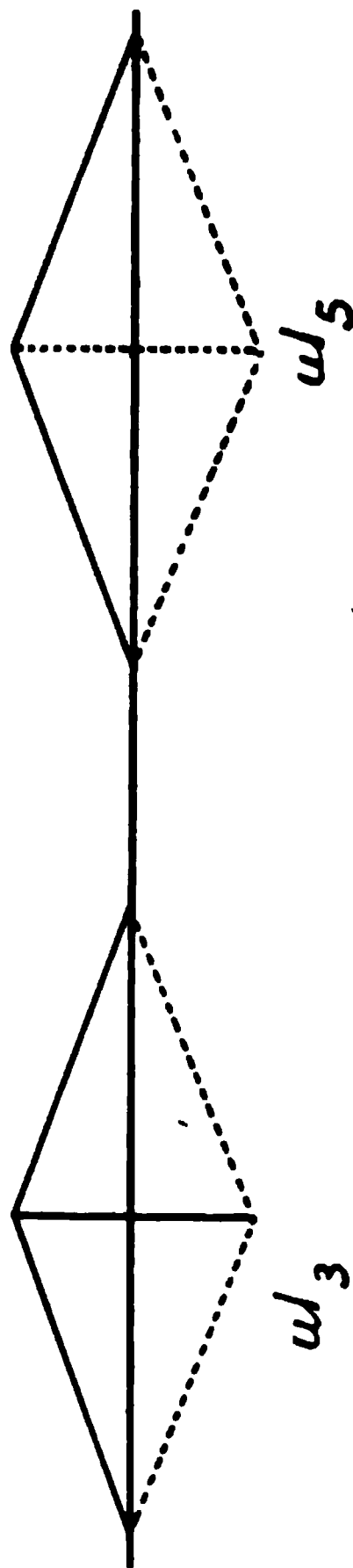


FIG. 5.

although a little distance off there may be another point undergoing greater pressure still. This little matter is not one which

is easy to describe, but mathematicians express it concisely by the equation—

$$\frac{dy}{dx} = 0.$$

In fig. 4, for example, there are two maxima, one at A and one at B.

Now, if in the sense of touch the mind only pays attention to the maximum point of stimulation of the nerve-terminations, it is highly probable that the same occurs in the sense of hearing,

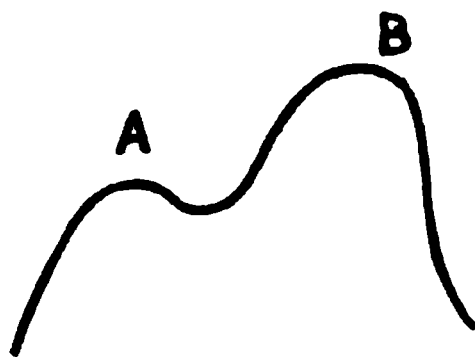


FIG. 4.

which, as remarked before, is only a delicate form of touch. This at once explains why, when a single tone is sounded, the mind should only be conscious of that tone even although other nerve-terminations are being stimulated.

Hitherto we have considered the movement of the basilar membrane and the response of the nervous apparatus only with respect to one simple tone. The subject becomes more interesting when we come to deal with compound tones, because it is here that theories are put to a more exact test.

To take the simplest case first. Let us suppose two simple tones at a considerable interval to be sounded, say  $ut_3$  and  $ut_5$ , then we are at once conscious of the co-existence of the two notes. In this case the movements of the basilar membrane would be exactly the same as those for a simple tone, but there would be two maxima as in the diagram (fig. 5, p. 335). One portion of the basilar membrane vibrates in response to the note  $ut_3$ , and another portion further towards the base of the cochlea responds to  $ut_5$ . There are thus two nerve-terminations stimulated to a maximum, and we hear the two notes corresponding to these nerve-terminations. So also, if three notes are sounded at considerable intervals, we get three points of maximum stimulation and hear three notes of corresponding

pitch. So far the case is practically the same as when only one simple tone is sounded. It should be observed, however, that when two or more pure tones at considerable intervals are sounded the result is not a mere noise. The sound may be discordant, but it is still clearly musical.

The interest begins when we have two or more notes sounded which are approximate in pitch. Let us take the case of a mistuned unison first.

Suppose we take two  $ut_3$  forks and mistune one of them so as to give four beats per second when both are sounded. Now the difference in pitch between these two notes is, as above stated, easily recognised if they are sounded separately, but when sounded together the sensation is that of a pure simple tone subject to the interruptions of the silences. It has been stated further that this is an objection to Helmholtz's theory because, if only two nerve-fibres corresponding to the two tones were stimulated, we should be able to note the difference much more easily when the notes were sounded together than when they were sounded separately. This we know to be true of the sense of sight; for example, two shades of a colour may be so close that we cannot tell the difference if they are seen apart, but recognise it at once if we see them together.

If we examine the movements of the basilar membrane in response to the two notes of a mistuned unison according to the theory proposed in this paper, we shall find that the movements produced in the membrane by one note will interfere with those produced by the other note. For example, suppose we sound two notes, one of 256 v.d. and one of 260 v.d. per second, then a certain portion of the basilar membrane will be acted on by both notes; in fig. 6 all that portion lying between the letters H and J will obviously be affected by both notes. Expressed in another way, we may say that any point between H and J will move with an amplitude equal to the sum or difference of the two amplitudes with which it would move in response to each note sounded separately. Thus take any point K; in response to the note of 256 v.d. it would vibrate with an amplitude represented by the line KP, and in response to the note of 260 v.d. it would vibrate with an amplitude represented by the line KO; when both notes were sounded together, and if at any

given moment the maximum displacements of the point were both above the position of rest, the point would vibrate with an amplitude represented by  $KP + KO$ . If both displacements were below the position of rest the movement would occur below the line of rest, and the amplitude would be represented by  $-(KO + KP)$ . If one displacement was above and the other below the position of rest, then the amplitude of movement would be represented by  $KP - KO$ , or  $KO - KP$ , and would be

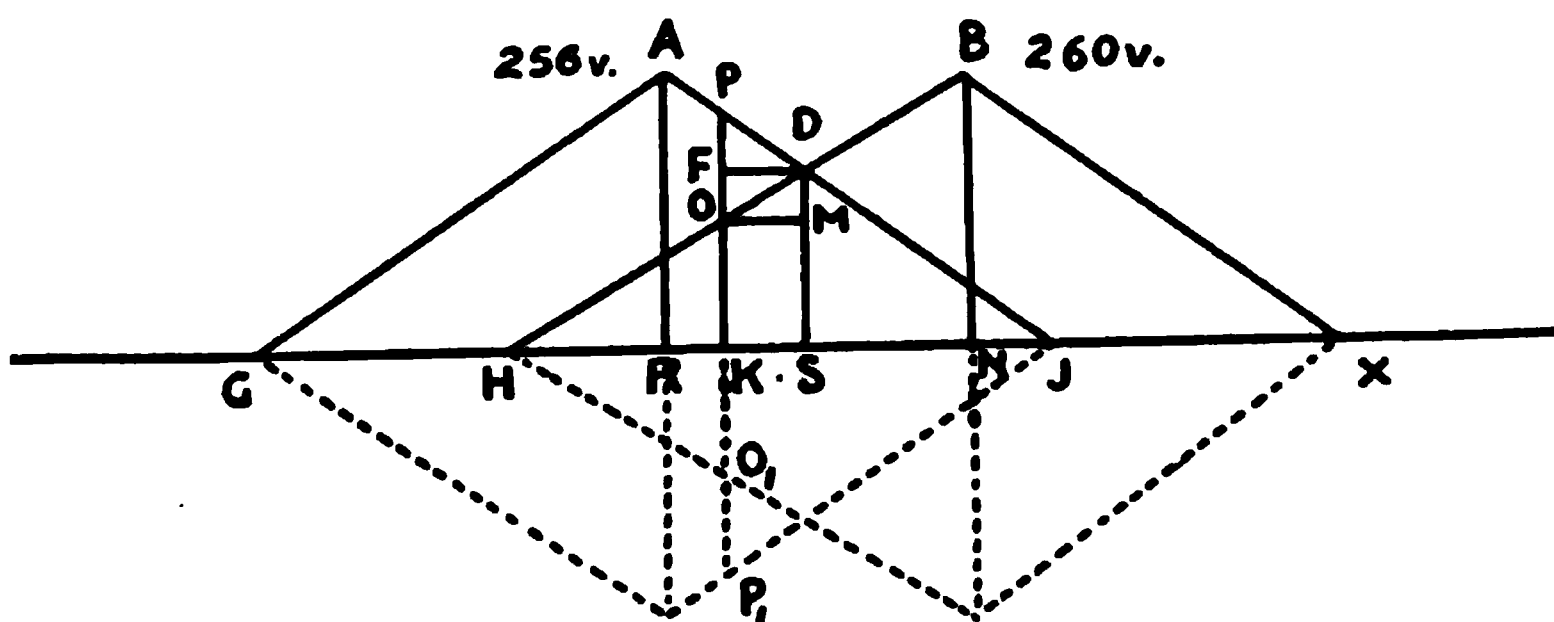


FIG. 6.

above or below the position of rest, that is, would be  $+$  or  $-$  in co-ordinate geometry, according as  $KP$  or  $KO$  were the greater.

We can find out the amplitude with which any point between  $H$  and  $J$  will vibrate as follows:—

First, suppose the intensities of the two notes to be equal, as in fig. 6, so that  $AR = BN$ . Since the notes are so close in pitch we may assume that the portions of the basilar membrane raised by each note separately would be equal, *i.e.*  $GJ = HX$ .

The amplitude of movement of the point  $K$  is represented by  $KO + KP$ . Let  $D$  be the point at which the two sides  $AJ$  and  $BH$  of the two equal triangles  $AGJ$  and  $BHX$  intersect; from  $D$  draw  $DF$  parallel to  $KS$ . The triangles  $OFD$  and  $PDF$  are equal in every respect.

$\therefore OF = PF$ . Draw  $OM$  parallel to  $KS$ .

$KO = SM$  and  $FO = DM$ .

$\therefore KO = DS - FO$ .

Similarly  $KP = DS + FP = DS + FO$ .

$\therefore KP + KO = 2 DS$ .



Now wherever  $K$  be taken between  $R$  and  $N$ ,  $FP = FO$ , therefore the amplitude at  $K$  is always equal to  $2 DS$  so long as  $DS > \frac{1}{2} AR$ . But  $2 DS$  is the amplitude of the movement at  $S$ , and  $S$  is a point midway between  $R$  and  $N$ , the points of the maximum amplitudes of the movements of the membrane caused by two notes separately. Therefore the maximum movements of all the points between  $R$  and  $N$  are equal, and when the phases of the two notes are in perfect agreement there will be no maximum *point* of movement, but a very small *section* of the basilar membrane will undergo maximum movement. Or, if  $y$  be the ordinate and  $x$  the abscissa of any point of the membrane between  $R$  and  $N$ , when it is displaced as described, then—

$$\frac{dy}{dx} = 0.$$

This, I think, is the reason why we cannot analyse the two notes of the mistuned unison when they are within close beating distance and sounded together, although we can distinguish them if sounded separately. In the first case the maximum pressure is never constantly at one point, but oscillates between  $R$  and  $N$ . In the second case, of course, the point of maximum pressure is constantly at  $R$  or  $N$  according to the note sounded.

The case discussed is that in which the intensities of the two notes are equal, and where the point midway between their two points of maximum amplitude vibrates with an amplitude of at least one-half the amplitude of movement of either of the maximum points produced by either note singly; or, as in the figure,  $DS > \text{or } \frac{1}{2} AR \text{ or } BN$ . Changes in the coefficient of elasticity have been neglected, as the introduction of this factor would only complicate the matter, and it does not affect the principle of the theory.

When the intensities are not the same and the intervals as before, then the condition of affairs is slightly different from that described.

Let  $R$  and  $N$ , fig. 7, be the two points of maximum amplitude of movement of the membrane when the two notes act separately, and let  $S$  be the point of the membrane upon which they both act equally, and let  $SD = a$  be the amplitude with which the points would vibrate in response to either note singly, so

that under the influence of both notes together it would vibrate with an amplitude of  $2a$ . Let  $\theta$  be the angle formed by the line of rest and the position of the basilar membrane when at its greatest displacement in response to one note, and let  $\theta_1$  be the angle formed by the line of rest and the basilar membrane at its greatest displacement in response to the other note. Let

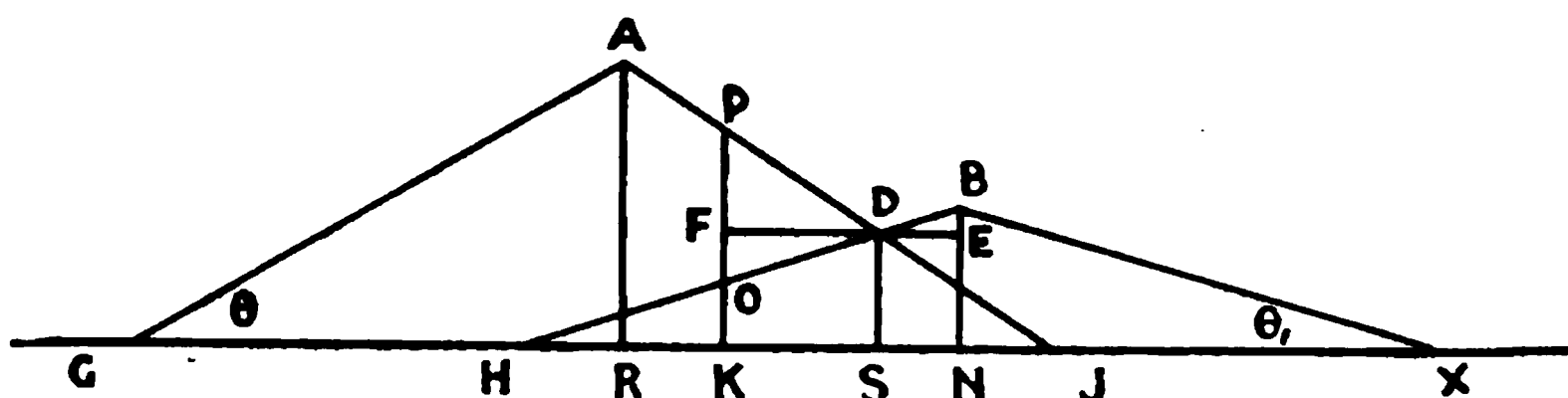


FIG. 7.

$RS = b$ , and take any point  $K$  between  $R$  and  $S$  and let  $RK = x$ . Draw  $EDF$  parallel to  $RN$  and draw  $PK$  perpendicular to  $RN$ , intersecting  $HB$  at  $O$  and  $EDF$  at  $F$ . Then in response to both notes the point  $K$  will vibrate with an amplitude represented by:

$$KO + KP = DS + FP + DS - OF. = 2DS + FP - OF. \quad OF = FD \tan \theta_1 \text{ and } FP = FD \tan \theta, \text{ and } FD = KS = b - x \text{ and } DS = a, \\ \therefore KO + KP = 2a + (b - x)(\tan \theta - \tan \theta_1).$$

Let  $y = KO + KP$ , then:—

$$\frac{dy}{dx} = \tan \theta_1 - \tan \theta.$$

It is evident from inspection that the point of maximum amplitude of movement is  $R$ , and the point of maximum pressure on the nerve-termination is therefore at  $R$ . But the pressure at  $R$  relative to the pressure at the other points is not the same as when a single note is sounded; the relative pressure will vary evidently according to the relative intensity of the two notes. In fig. 7 there is rapid increase in the movement and therefore of the corresponding pressure from  $G$  up to  $A$ , then a slow decrease from  $A$  to  $B$ , followed by a rapid decrease from  $B$  to  $T$ .

The description just given according to the writer's suggestion has been applied only to the movement of the basilar membrane upwards; the movement downwards is, of course, just a reverse copy of that upwards.

Hitherto we have considered a mistuned unison where there has been either no point of maximum amplitude or one in which the slope from the maximum amplitude was very slight on one side; or, using the notation of the differential calculus:

$\frac{dy}{dx} = 0$ , or a relatively small differential. Further, the section

of the membrane undergoing this vibration is very small, so small indeed as closely to approximate to a point, and we therefore hear a pure musical tone, interrupted of course by the silences; but we do not hear two musical tones, because there are not two points of maximum amplitude.

We now proceed to consider the condition of matters which will occur when the two notes become separated by a greater interval. First let us suppose the intensities equal. In this case the points of maximum movement of the two notes separately will be wider apart, but as long as DS (fig. 6) is greater than  $\frac{1}{2}$  AR or BN there will still be no *point* of maximum amplitude, but a *section of the membrane* undergoing a movement of maximum amplitude. Further, it is clear that as this section of the membrane becomes greater the amplitude of its movement becomes less. Now this quite agrees with what we find from experiment, for in a mistuned unison the fewer the beats the louder do they become. The fact, however, may perhaps be explained by physical causes acting in the air.

As the notes become still more widely separated, DS becomes less than  $\frac{1}{2}$  AR (or BN), as in fig. 8 (p. 345), and now there are two points of maximum amplitude, and we now begin to be able to analyse the sound into its two constituents. It is probable, however, that even for some interval after two points of maximum altitude appear, we are still unable to analyse the compound tone into its constituents, because the dip between the two points is still inconsiderable, and the difference in pressure upon the nerve-terminations correspondingly slight.

Before proceeding further we may again compare the two senses of hearing and touch. When a single pure tone was sounded we saw that it had its analogy in touch when there was contact at a single point on the skin. Have we, then, an analogy in the sense of touch corresponding to the sensation experienced by the ear when two notes at a very slight interval are sounded?

There is no doubt that we have, for it is well known that if the skin is stimulated at two points close together we are not able to distinguish them (*Physiology of the Senses*, M'Kendrick and Snodgrass, p. 54). Thus at the tip of the finger the minimum distance at which two points can be perceived as such is 2-3 mm. In other words, the mind is not able to analyse the variation in pressure, which is in complete agreement with what we find in the case of listening to a mistuned unison. But the similarity between the two senses is even closer, for from experiment the writer has found that the skin of the finger-tip perceives a change in the locality of the stimulation at a distance far less than 2-3 mm. If a point of a needle be pressed gently against the finger-tip, and then be moved and made to press against another point of the skin at about a distance of 1 mm., or even less, we are quite conscious of a change in the locality of the pressure. So that here also we have an analogy with the sense of hearing when we find that though the ear is not able to analyse a note composed of two simple tones if the interval is very small, yet it can recognise a change in the locality of maximum pressure if the two simple tones of the compound one be sounded separately.

So far, therefore, we have a complete analogy at all points between the sense of hearing and that of touch.

Now, as the two points of maximum amplitude of movement of the basilar membrane become further apart it is evident, from inspection of fig. 8 (p. 345), without showing mathematically, that the dip, so to speak, between the two maximum points becomes more and more pronounced, until ultimately the portion of the membrane vibrating in response to one note will not interfere at all with the portion vibrating in response to the other note. Of course the distance between two maximum points at which this may occur must be unknown, and may vary according to the pitch, though, for reasons which will be shown later, there is good reason to believe that at an interval of an octave the vibrating portions of the membrane are still interfering with one another.

When three or more notes are sounded at sufficiently distant intervals, so that their corresponding points of maximum movement in the basilar membrane are sufficiently far apart as not to

interfere too much with one another, then we are able to analyse the compound note into its three constituents, and so on for a larger number of notes. In these cases, of course, we have the analogy in the sense of touch that when two or more points of the skin sufficiently far apart are touched we are conscious of contact at two or more points.

The most interesting case is that in which several notes are sounded so near that there are no maximum points, or, at least, none sufficiently pronounced to be perceived as such, and yet sufficiently far apart that a considerable section of the

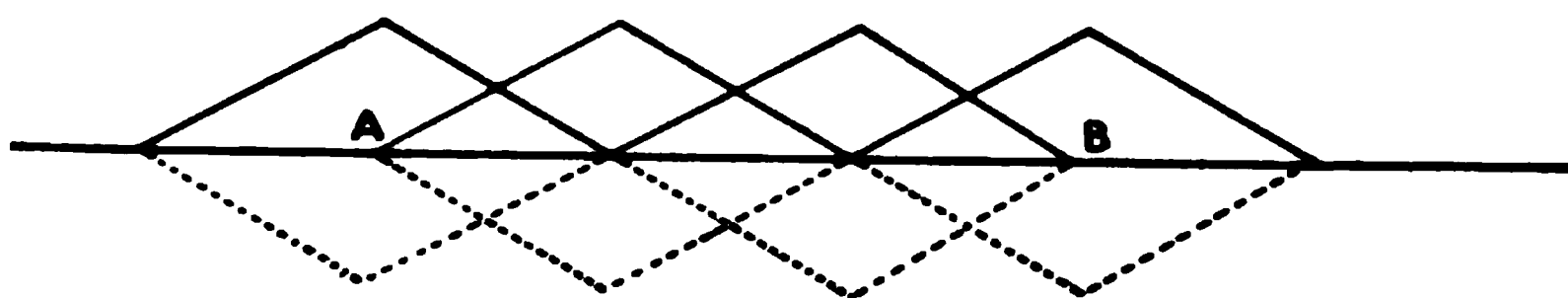


FIG. 9.

membrane vibrates with approximately equal amplitudes in all its parts. Such a case is shown in fig. 9, which represents the movements of the membrane in response to a compound tone produced by four notes of equal intensity at such intervals.

AB is the position of rest of the membrane (in this fig. the displacement both above and below the line of rest is represented).

Fig. 10 represents the resultant maximum movement when the phases are all in complete agreement; all the points in that portion of the membrane between A and B would vibrate with

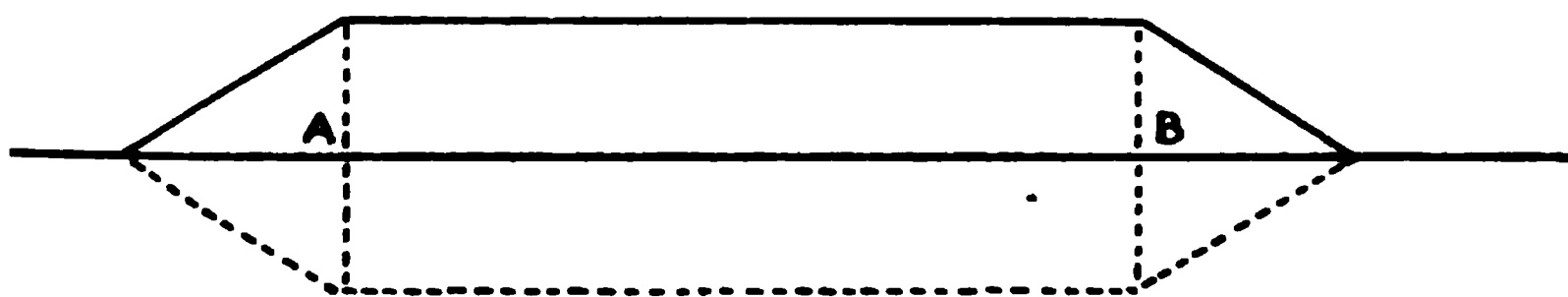


FIG. 10.

the same maximum amplitude. When the phases were not in agreement there would be a maximum point, but it would never for an instant remain constant in position but would oscillate between A and B, and, further, would never have as great an

amplitude of movement as that of the portion AB as a whole. The pressure upon the nerve ending in this case, as in the others, varies, of course, as the amplitude of the movement of the basilar membrane. Therefore, the maximum pressure would not be at a point, but along a line; that is, all the nerve-fibres, in connection with the hair-cells between A and B would be stimulated to the same extent. It corresponds, therefore, with pressure along a line in the sense of touch; in other words, with a sharp edge applied to the skin.

I believe that in this case the sensation we experience in the case of hearing is that of a noise. Nor is this entirely a matter of conjecture. In the experiment described at the beginning of this paper I described how, when the four tuning-forks (two  $ut_4$ ,  $si_3$ , and  $si_3b$ ) were mistuned so as to interfere with each other and produce rapid beats, and when they were bowed with the requisite intensities, the musical element in the sound was very small and the noisy element prominent. On the other hand, when four forks, each an octave above the preceding one, were weighted so as to produce rapid beats, the musical element predominated. Even in this case the slight element of noise is probably explained by the fact that the upper partials of the lower pitch-forks would have a vibrating-frequency closely approximating those of the highly-pitched forks. These experiments are, of course, rough, because of the difficulty of getting the suitable intervals and intensities. I am at present constructing a large series of pipes covering about an octave, and by this means I hope to investigate the causation of noise with more accuracy. The experiments, however, go to show that the sensation of noise is produced when a series of notes at no great intervals are sounded together with approximately equal intensities. Of course, if one or more notes predominate, then a more musical element appears, and this is fully explained by the theory proposed, because such a predominance of one note will call forth a corresponding increase in the amplitude of movement at a point in the basilar membrane.

On similar grounds it would appear that what is termed a discord in music, is produced in a similar way to a noise. In this case either the interval between the two notes themselves, or between some of their partials, is too small to allow of well-

pronounced points of maximum amplitude of movement of the membrane, or too large to cause merely an increase and diminu-

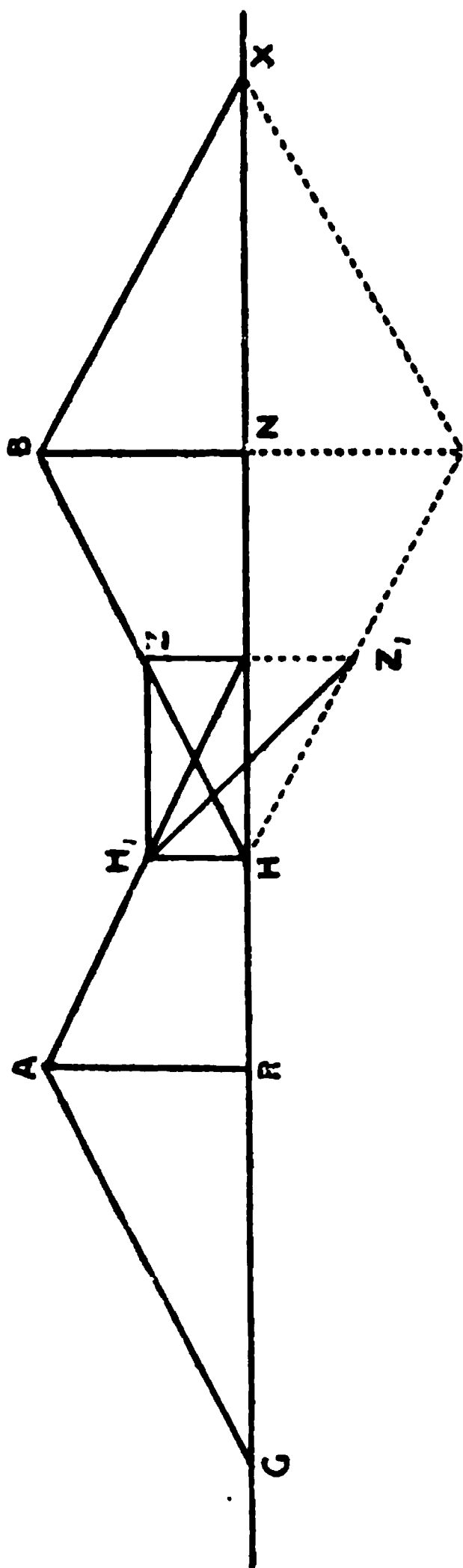


FIG. 8.

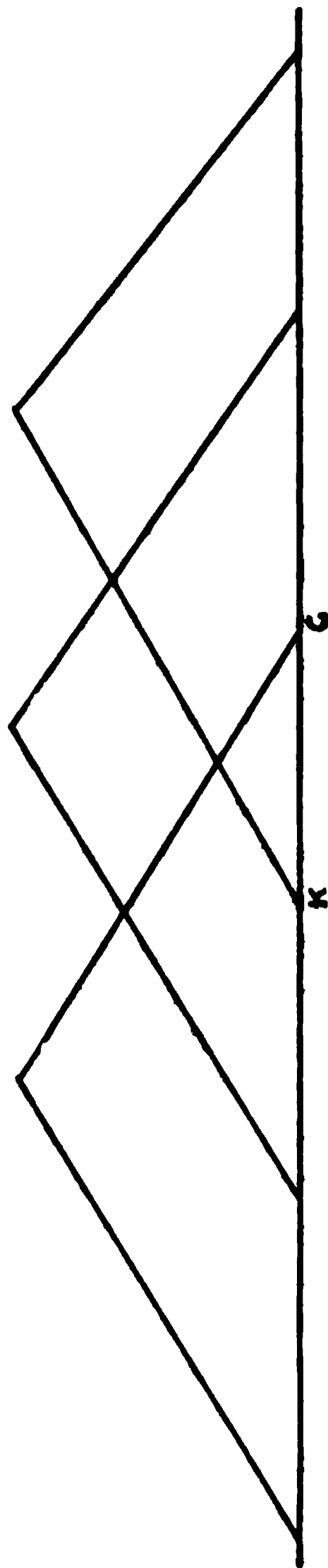


FIG. 11.

tion in the intensity of the musical sound, such as is produced by two notes within close beating distance. A discord, accord-

ing to this view, is a musical sound on its way to become a noise, and I think our sensations would bear out the statement above arrived at on theoretical grounds.

In relation to noise, it is very interesting to note that we are now in a position to see clearly why, although we cannot fix the exact pitch of a noise, we are yet quite conscious that noises have pitch relative to one another. Thus, if a small portion of the basilar membrane in the lower whorl of the cochlea were undergoing movement, such as that represented in fig. 10, we should not be able to give its exact pitch, because there is no point of maximum amplitude, but we would be conscious of the fact that it was of relative high pitch, because the nerve-terminations stimulated are in the part of the cochlea which responds to tones of high pitch; and so on for similar movements in other parts of the basilar membrane.

It has been shown in the preceding pages how close is the analogy between the sense of hearing and that of touch, according to the theory I have put forward. A point of contact in the skin corresponds to a simple musical tone. Two points of contact so close as to be indistinguishable from one point when both occur simultaneously, has its analogy in the ear in the case of a mistuned unison giving slow beats. And the fact that we can estimate change of locality over a distance in the skin smaller than the distance at which we can perceive two points, as such, simultaneously estimated, corresponds with the fact that we can tell the difference in pitch between two notes sounded separately, even though they be so close that we cannot analyse the compound tone which they produce when sounded together. And further, we have seen that a noise has its analogy in the sense of touch in the case of contact along a line or an edge.

There remains the question, what sensation have we in the case of the ear corresponding to contact of the skin over a surface? The answer of course is, that we have no such analogy in the case of hearing; and this for a very good reason. In the skin the nerves terminate over a surface; in the organ of Corti the nerve terminates along a line. We could not, therefore, have an analogy in the sense of hearing corresponding to the sensation of contact over a surface in the case of touch. This apparent exception, therefore, may be said to support the



close analogy between touch and hearing, as explained in the preceding pages.

There remains now only the consideration, how does the theory agree with the fact shown by Lord Kelvin, that under certain circumstances the ear is able to appreciate change of phase? Helmholtz's theory does not explain this.

Taking first the case of a mistuned unison giving slow beats (fig. 6). Since the maximum points are close together, it is evident that changes of phase will merely cause an increase or diminution in the intensity of the sound, because the portions of the basilar membrane acted on by the two notes are almost identical.

When, however, the interval becomes greater, the basilar membrane begins to be acted on in a more irregular manner. Thus, in fig. 8 the membrane is raised from G to A, then it slopes down with the same inclination from A to  $H_1$ ; now at this point a change in the sharpness of the inclination will occur. For, if the displacements of the membrane produced by the two notes are in the same direction, then the inclination will become less sharp, as, for example, from  $H_1$  to Z. If the displacements are in the opposite direction, the inclination will become more abrupt, as from  $H_1$  to  $Z_1$ .

Now, if the cycle is completed very rapidly, as in a perfect harmony, *e.g.* an octave, these changes will be so rapid that we cannot perceive them, but if the cycle is changed slowly, then a given displacement of the membrane will only recur at relatively long intervals, and the mind is able to appreciate the variations in pressure upon the nerve-terminations. This occurs when the harmony is imperfect. We see here, therefore, the explanation why the ear appreciates change of phase only on imperfect harmonies other than unison.

Lord Kelvin further noticed the fact that these changes of phase were much more pronounced in the case of mistuned multiple harmonies than mistuned binaries, except the binary octave. Now, according to the theory proposed, it is clear that if we used three notes, each of which acted in part upon the same portion of the basilar membrane, the movements would be still more pronounced, and the pressure variations on the nerve-terminations would be more marked.

Thus in fig. 11 the portion of the membrane between K and G would be subject to very great variations in the extent of its movements, and its inclination to the line of rest and the nerve-terminations would be subjected to very pronounced variations in pressure. As in the case of a binary harmony, it is essential that the cycle should change slowly.

As the intervals become greater than an octave, the ear gradually becomes less able to perceive difference of phase. Thus if the harmony 1:3 be mistuned, the change of phase during the cycle is by no means so easily perceived by the ear (Lord Kelvin, *loc. cit.*), and as we pass to greater intervals, still the ear no longer perceives a difference in the character of the sound produced by differences of phase. It is the fact that the ear can perceive these differences at intervals of an octave, and even a little more, that leads the writer to the conjecture that the portion of the basilar membrane which responds sensibly to a single note, covers at least an octave. That is to say, if a certain note produces a maximum movement of the basilar membrane at a certain point, then the membrane is vibrating sensibly, though, of course, with much less amplitude, at a point which would be the maximum amplitude of movement called forth by the octave of the note referred to. This is, however, as remarked above, a matter of conjecture.

In the preceding pages it has been shown how the basilar membrane may analyse compound tones into their constituent simple tones, and how under many circumstances, such as noises and mistuned unisons, this analysis does not occur, or at least very imperfectly. It now remains to find out by what means these variations in the amplitude of the movements of the basilar membrane are transformed into nervous impulses. The mechanism by which this is done appears to be simple and singularly beautiful.

Since the hair-cells follow every movement of the basilar membrane, then, in their upward displacement, the hairs, and even to some extent the cells themselves, will be pressed against the tectorial membrane which, in the living condition, lies like a pad over them. In fig. 1 this is not shown, because the section was prepared by the celloidin method which necessitated dehydration, but in sections cut in gum or by other methods without dehydration, the fact is very clearly seen.

When, therefore, the hair-cells are raised against the tectorial membrane, the latter will resist their upward progress and press them down against the nerve-terminations at their bases. Further, the greater the amplitude of movement of the basilar membrane, the greater will be the pressure of the hairs and hair-cells against the tectorial membrane, and the greater will be the stimulation of the nerve-fibre at the base of the hair-cell. When, therefore, a pure tone calls forth a movement of the basilar membrane as in fig. 3, a considerable number of nerve-fibres will be stimulated, but the intensity of the stimulation will be greatest in that nerve-termination which lies at the base of the hair-cell opposite the point of maximum movement of the basilar membrane. In the same way the movements of the membrane called forth by compound tones and noises are transferred into pressures upon the nerve-terminations. Now no more perfect means could be devised for this purpose than the tectorial membrane. It is not attached to the vibrating portion of the cochlea, and it lies over the hairs like a pad, so that the more they are projected upwards against it, the more firmly does it press the hair-cell down against the nerve-termination.

By this means, therefore, the variations in amplitude of movement of the basilar membrane become transformed into exactly corresponding variations of pressure upon the nerve-terminations. These variations of pressure are then sent to the brain, and there analysed in exactly the same way as the pressure variations in the sense of touch are analysed. In fact, the auditory nerve may be looked upon purely as a nerve of touch, but vastly more delicate than any of the other nerves of touch. This is to be expected, for the supply of nerve-fibres to the organ of Corti is far richer than to any part of the skin of corresponding dimensions.

This theory of maximum amplitudes, as it may be termed, appears to account for the known facts concerning the sense of hearing as completely as the theory of Helmholtz, of which it is a modification; and the objections urged against the latter theory cannot be urged against it. Thus many will not admit that each fibre of the basilar membrane or each arch of Corti can move independently of those adjacent to it, which

Helmholtz's theory requires. This objection cannot be urged against the theory proposed in this paper.

Again, Helmholtz's theory does not explain the existence of noise, unless the latter be regarded as purely psychological; and even if that were admitted it does not explain why we cannot, under any circumstances, analyse a noise into its constituent simple tones. The theory proposed in this paper is exactly the reverse in this respect, for supposing it to be correct, then a sound is a noise when we cannot analyse it into its simple constituents; and if we are able to analyse, whether entirely or only partially, then a musical element appears.

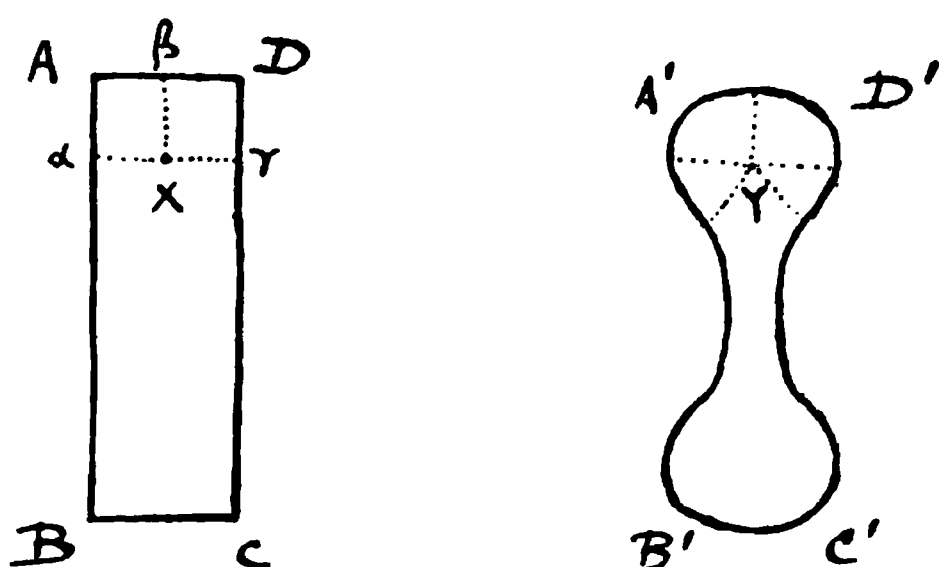
In this theory of hearing we have seen a remarkable analogy between that sense and the sense of touch.

The pathological facts concerning the loss of high tones with disease of the lower whorl of the cochlea is equally explicable by either this theory or that of Helmholtz.

ON THE CAUSES OF THE SHAPE OF NON-NUCLEATED  
RED BLOOD CORPUSCLES. By W. MYERS, M.A.,  
M.B., B.Sc., *John Lucas Walker Student in the University  
of Cambridge.*

THE peculiar biconcave shape of non-nucleated erythrocytes is of very wide distribution, since it is, generally speaking, characteristic for mammalia. It is the object of this paper to give a physical explanation of this striking phenomenon.

For the function of the red corpuscles as carriers of oxygen, the biconcave disc is a very advantageous form, for in a disc with concave sides the relation of surface to volume is greater than in a flat disc.



If, for example, A, B, C, D and A', B', C', D' represent median sections of two such discs, with equal diameters, since A', B' is longer than A, B, and since the dumb-bell shaped area A', B', C', D' is less than the rectangular area of the left hand figure, it is evident that the biconcave disc has a considerable adaptation to rapid diffusion.

We may notice a further advantage by the following considerations:—Let us take a point  $\gamma$  in the centre of the upper knob of the figure A', B', C', D'. It is obvious that  $\gamma$  is at a distance of  $\gamma$  A' from the periphery in most directions. Only in a small segment does the thin middle part of the disc make  $\gamma$  at a greater distance. In other words,  $\gamma$  is at the centre of a circle, which is incomplete for a small fraction of its periphery.

If, however, we take a similar point X in the flat disc, in only three directions is it as near the periphery as  $\gamma$  in the other figure; namely, in  $X\alpha$ ,  $X\beta$ , and  $X\gamma$ . In all other directions it is further from the periphery.

The opinions which are held on the structure of these corpuscles are so various that it is almost impossible to take any view without being opposed to some physiologist of high standing. This is mainly due to the difficulties of interpretation of microscopic observations. The question, for example, of the presence of an enveloping membrane has been widely discussed, and from purely microscopic evidence must be regarded even now as undecided. Largely owing, however, to the work of Hamburger on the isotonic point of the corpuscles, the opinion that there is a membrane has gained ground; and it may be mentioned that authors who deny its existence, such as Hayem, yet admit that the centre of the corpuscle is more fluid than the periphery. In this paper the presence of a membrane will be assumed. The argument for it has been simply and strongly put by Ehrlich, whose words may here be quoted. He says<sup>1</sup>: "Beginnen wir . . . mit der Frage, warum sich die rothen Blutkörperchen im Blutserum nicht auflösen, so leuchtet ohne Weiteres ein, dass dies nur dadurch geschehen kann, dass das Hämoglobin der Blutscheibe, das ja im Serum leicht löslich ist, von diesem durch ein diffusions-verhindernde Membran getrennt sei."

With regard to the structure of the protoplasm of the corpuscle there is more uniformity of opinion, and the view is now generally held that no structure can be observed in the normal corpuscle. Further, biconcave non-nucleated discs are characteristic for mammalia *in corpore*, and are not merely artefacts.

In considering the shape of the non-nucleated discs it must be borne in mind that they are biconcave not only in normal conditions, but that the poikilocytes of various forms of anæmia, and the poikilocytes which can be produced by carefully heating healthy blood, are also biconcave. Any attempt to account for the biconcavity of the erythrocytes must explain that of the poikilocytes also.

The following hypotheses have been put forward to explain the biconcavity of the red blood corpuscle:—

<sup>1</sup> *Charité Annalen*, Bd. x.

1. *Mechanical*.—That the concavity is caused by one disc coming in contact with another, and with the vessel walls as the blood circulates, so that portions are worn away from an originally flat disc. This hypothesis is unsatisfactory, inasmuch as the circumference of the disc is more exposed to friction, while the centre is supposed to be worn down. This difficulty may of course be overcome by assuming that the discs are composed of parts of greater and less resistance, the centre being less resistant. There is, however, no histological evidence of any such difference.

2. *Morphological*.—That the protoplasm of the corpuscle possesses in itself the power of assuming a biconcave form. Clearly this is more a restatement of the facts than an explanation, and is open to the further objection, that, as a general rule, protoplasm alone has not morphological properties. Verworn has shown for low forms of life that the nucleus exercises a morphological influence over the rest of the cell, and that when a portion is cut off from the nucleus, it may, in a limited sense, live for a time, but is now deprived of morphological properties. Admitting that the red non-nucleated discs can retain the form imparted to them by their nucleated parent cell, the biconcave poikilocytes, one generation removed from the nucleated cell can hardly be supposed to have morphological endowment therefrom. And we should still less expect that the highly differentiated protoplasm of the nucleated red corpuscle should have morphological properties which the 'generalised' protoplasm of simple unicellular organisms does not possess. Supposing, then, that this hypothesis were true, inasmuch as it would constitute an exception to a general biological law, it would itself require a special explanation.

3. *Teleological*.—A biconcave corpuscle has the advantage over a disc with plane sides of the same volume, that it affords an increased surface for oxygen diffusion. Though we can thereby understand why so many animals possess corpuscles of this shape, a teleological explanation brings us no clearer perception of the processes by which this shape is attained.

No one of these theories is satisfactory, and it seems natural to seek the causes of the biconcave shape in the structure of the corpuscle and its surrounding conditions.

When the corpuscles are placed in hypotonic sodium chloride solutions they lose their hæmoglobin, and the serum or plasma becomes laked. On putting a drop of blood into slightly hypertonic salt solution on a microscopic slide under a cover-glass, by allowing a drop of distilled water to touch the edge of the cover-glass, the microscopic appearances of hæmolysis can be observed. The first change that can be noticed in a corpuscle is an increase in size, generally uniform, so that the face of the corpuscle remains circular. Soon after this swelling has begun the biconcavity becomes less distinct. The two changes proceed until finally a round disc is produced, in which no biconcavity can be observed. This disc then loses distinctness, and gradually passes to the 'shadow,' which can only be seen with difficulty. The loss of distinctness proceeds more slowly than the swelling and loss of the biconcavity.<sup>1</sup>

The rate of these changes varies with the proportion of water that is added. If this be large, the corpuscles are so rapidly hæmolysed that it is impossible to watch the process; and it is only when the fluid surrounding a corpuscle is but slightly hypotonic, that the process above described can be observed.

The point I would emphasise is this, that by putting the corpuscles under conditions where they can take up water, loss of biconcavity of the disc is to be observed.

On dehydration, on the other hand, the biconcavity is exaggerated. This is shown by the comparison of the corpuscles in salt solution, and in dry preparations, by Ehrlich's method. In the latter the biconcavity is well marked, and not infrequently corpuscles may be seen with a quite clear centre. Such corpuscles may be observed in unstained specimens or even in films stained with eosin.

This increase of the biconcavity of the corpuscles on dehydrations is an old observation of Hayem's, whose own words may be given<sup>2</sup>:—"Ajoutons, en terminant, que par l'étude des propriétés optiques des hæmaties desséchées, la forme biconcave des hæmaties est rendue très évidente.

"Quand la préparation a été faite avec une grande rapidité et

<sup>1</sup> It may be mentioned in passing that similar appearances result from the action of some hæmolytic toxins.

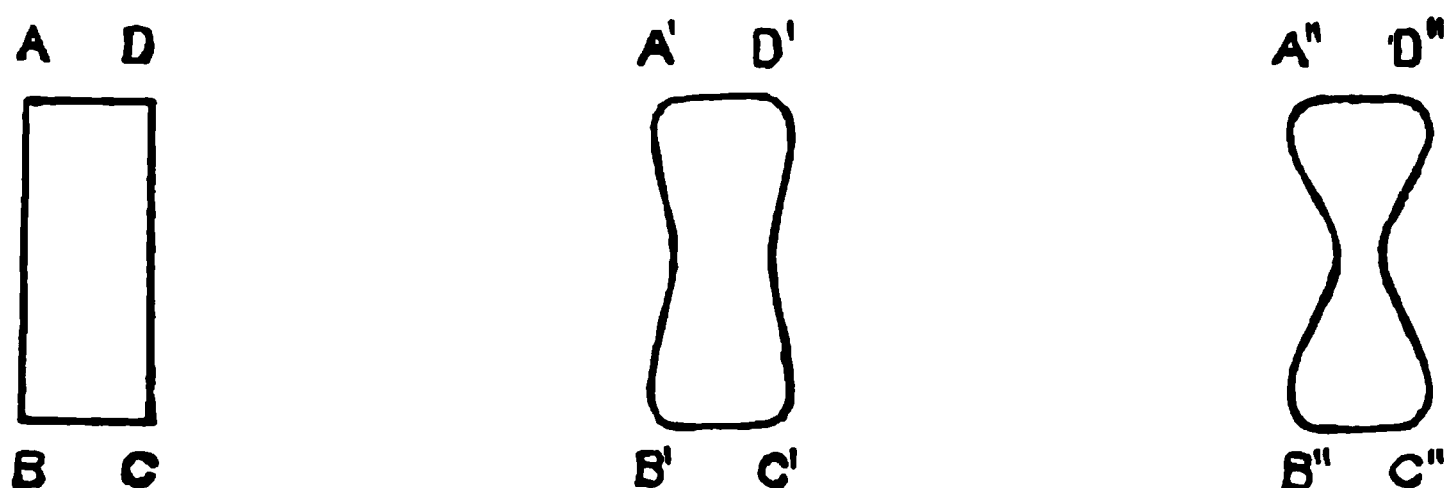
<sup>2</sup> Hayem, *Du Sang*, p. 80.



avec du sang parfaitement normal, un bon nombre de globules rouges sont uniformément colorés, et à peine plus épais sur les bords, qu'au centre. Mais à côté d'eux, on en trouve toujours dont le centre est clair, à cause du retrait plus ou moins complet de l'hæmoglobine sur le bord épais."

The corpuscle, then, in the condition in which it occurs in the blood may be made to lose its biconcavity when the fluid surrounding it is hypotonic; and its biconcavity is increased on desiccation to a moderate degree.

This behaviour of the corpuscle can be explained by a simple hypothesis.



The figure A, B, C, D represents a median section of a circular disc. We will suppose the disc to be enveloped by a pliable membrane, which is capable of extension, but which is incapable of contraction. The contents of the disc we will suppose to be liquid.

If we diminish the amount of fluid in the disc, say by osmosis, the volume the disc contains becomes less, but since the membrane is incapable of contraction, a change of shape ensues. The shape, with a moderate degree of diminution of volume, is shown by the figure A', B', C', D'. On abstracting more fluid from the disc, the biconcavity becomes more marked, as in the figure A'', B'', C'', D'', until ultimately the two side walls meet.

The corpuscle in the blood represents the stage A', B', C', D'; on drying, the biconcavity becomes more marked; and we may even get an apparent meeting of the two side walls, as shown by the corpuscles in a dried slide, which may show a clear unstained centre. [It may be noted in this connection that corpuscles of

this shape occur in some forms of anæmia, and are known as 'pessary' forms.<sup>1</sup>]

When, however, the corpuscle absorbs water, the biconcavity disappears, and we get the form A, B, C, D. In other words, within certain limits the corpuscle behaves as if it had fluid contents, and were surrounded by a pliable membrane, which was capable of extension, but not of contraction. The question now arises, do we know of any cause determining the form in which these corpuscles are present in the blood? Why is the corpuscle biconcave, and not flat?

The extreme sensitiveness of the corpuscles to external conditions is shown by many facts. We can estimate, for example, the strength of certain salt solutions to hundredths of a gram per cent., when they are used as indicators. Again, large quantities of corpuscles may be completely hæmolysed with minute amounts of toxins or inorganic poisons. Perhaps most remarkable is their selective power for certain substances in the fluid around them. Potassium, manganese, and iron salts are not absorbed by them; grape sugar, on the other hand, readily passes into their substance. So delicate are these reactions that some authors see in them a display of the vital activity of the protoplasm of the disc. Be this as it may, the necessity for a consideration of the plasma in any attempt to account for the corpuscles is evident.

The blood plasma is so complex a fluid that our present means of analysis are quite inadequate to give a full account of its composition. In the last few years, for example, a number of previously unknown substances—bacteriolytic, hæmolytic, agglutinating, antitoxic—have been found in normal sera. The osmotic behaviour of such a fluid *in corpore*, we can only picture from simple physical experiments, and probably imperfectly. Hamburger, however, has established the important fact that the plasma of a blood, in many cases at least, is hypertonic for its own corpuscles. In other words, the osmotic pressure within the corpuscles is less than that of the plasma.

Here, then, we have a fact which is fully capable of explaining the biconcave shape, for, bearing in mind the sensitiveness of the corpuscles to external conditions, we cannot suppose that

<sup>1</sup> Litten, *Berl. Klin Wochenschrift*, 1877, No. 1.

a hypertonic fluid, such as the plasma, is without influence on them.

The hypothesis I venture to propose is, that the biconcave shape of the corpuscle represents an early stage of dehydration of a disc which contained more water, the dehydration being brought about by the plasma. The corpuscles behave within limits as if they were composed of a membrane incapable of contraction, with fluid contents. The addition of water causes obliteration, and slight dehydration exaggeration of the biconcavity.

To show directly that the red corpuscles at their origin have flat sides, and become biconcave by loss of water, is with our present methods impossible. The doctrine of the development of red discs from nucleated cells, for instance, is based on indirect evidence; and, further, the only reliable method at the present time for examining blood is that by means of dry preparations, introduced by Ehrlich, which is obviously out of court for the present purpose.

Further, we must suppose that the red discs when first produced contain the same proportion of water as the nucleated cells from which they are cut off. Now it is quite impossible to calculate how much water a disc must lose in order to become biconcave. But it is readily conceivable that it may be too little to be appreciable. So that, should it be found that the isotonic point of the nucleated red cells was indistinguishable from that of the daughter discs, this would not disprove the hypothesis. But, so far as they go, the data known at present support it. For in cases of severe secondary anæmia, and in pernicious anæmia, large quantities of nucleated red blood corpuscles are present in the blood. And in these cases the isotonic point of the corpuscles is abnormally low.<sup>1</sup>

The formation of the central depression in a poikilocyte is brought about in the same way as in the mother disc. An objection may be raised that since the osmotic equivalents of the mother and daughter disc are identical at the time of separation, if the mother disc was in equilibrium with the plasma, why should the daughter disc, on being cut off, become further dehydrated? It may be pointed out, in the first place,

<sup>1</sup> Ehrlich and Lazarus, *Die Anæmie*, Bd. i.

that the small poikilocyte possesses a greater surface relatively to its volume than the mother disc, and would therefore more readily lose water. And, secondly, we must suppose some circumstance in the corpuscle by which it is enabled to remain in equilibrium in a plasma that is hypertonic. The readiest supposition is that the outer layers contain less water, and therefore for some reason offer a resistance to the passage of more water out into the plasma. With a mechanism such as this, since it would be disturbed on the cutting off of a poikilocyte, we can easily understand that the poikilocyte, on becoming free, at once loses water.

This hypothesis of the normal shape of the non-nucleated red corpuscle would attribute to the possession of a hypertonic plasma an additional advantage to those already recognised. A hypertonic plasma protects the corpuscles, in so far that a passing increase in the water it contains, an increase afterwards compensated, may take place without any laking of the corpuscles *in corpore*. And, further, the action of some hæmolytic poisons, *e.g.*, snake venom, eel's serum, is diminished in a hypertonic salt solution. And on the hypothesis here put forward, the hypertonicity of the plasma plays an important part in the causation of the shape of the red corpuscles, a shape which, as indicated at the beginning of this paper, shows a high adaptation to their function.

In conclusion, I wish to express my thanks to my friend Mr W. M'Dougall for valuable criticism.

THE ANTERIOR LIMIT OF THE CERVICO-THORACIC  
VISCERAL EFFERENT NERVES IN MAN. By N.  
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I.—THE CERVICO-THORACIC RAMI COMMUNICANTES.

THIS research is a continuation of the examination of the limits of outflow of visceral efferent nerves, of which two sections have been published in this Journal, on the Lumbar Rami (12), on the Pelvic Splanchnics (13).<sup>1</sup>

1. *The Rami in Lower Animals.*

The results of the many investigations made upon these nerves by experimental and fine anatomical methods are dealt

<sup>1</sup> A grant in aid of the expenses of the researches embodied in these three papers has been made by the Scientific Grants Committee of the British Medical Association.

with exhaustively by Langley (16), in the report of his examination of this region in the cat, dog, and rabbit. It is therefore unnecessary for me to enter here into the literature of the subject in detail. As a means of comparison between the results obtained for man in the present research and those obtained for other animals, the results of the more important observations are classified :—

TABLE I.

| Observer.                   | Date. | Animal.                | Methods.   | Anterior limit of reaction. | Highest level at which white bundles were found. |
|-----------------------------|-------|------------------------|--|-----------------------------|--|
| Budge (3)                   | 1852  | Rabbit                 | Stimulation of spinal roots                      | Thoracic I.                 | ...  |
| do. (4)                     | 1853  | do.                    | Excision of segment of spinal cord               | Cervical VIII.              | ...  |
| do. (5)                     | 1855  | do.                    | Stimulation of spinal roots                      | do. VI.                     | ...  |
| Bernard (2)                 | 1862  | Dog                    | do.  | Thoracic I.                 | ...  |
| Salkowski (20)              | 1867  | Rabbit                 | Cutting spinal roots                             | Cervical VII.               | ...  |
| Ferrier (9)                 | 1883  | Ape                    | Stimulation of spinal roots                      | Thoracic II.                | ...  |
| François-Frauck (10)        | 1878  | Cat                    | Stimulation of rami com.                         | Cervical V.                 | ...  |
| Navrocki and Przbylski (17) | 1891  | do.                    | do.  | do. VIII.                   | ...  |
| Dastre and Morat (7)        | 1883  | Dog                    | Stimulation of rami com. or spinal roots         | do. VIII.                   | ...  |
| Gaskell (11)                | 1886  | Dog                    | Dissection and serial sections                   | ...                         | Thoracic II.                                     |
| Sherrington (16, p. 89)     | 1892  | Ape                    | Stimulation of spinal roots                      | Thoracic I.                 | ...  |
| Langley (16)                | 1892  | Rabbit,<br>Cat,<br>Dog | Stimulation of spinal roots and fine dissections | do. I.<br>do. I.<br>do. I.  | Thoracic I.<br>do. I.<br>do. I.                  |

TABLE II.—*Analysis of Observations.*

| Limit of Outflow. | No. of Sets of Observations. |
|-------------------|------------------------------|
| Cervical V.       | One                          |
| Do. VI.           | One                          |
| Do. VII.          | One                          |
| Do. VIII.         | Three                        |
| Thoracic I.       | Nine                         |
| Do. II.           | Two                          |

The summary of results obtained from the examination of these four animals, cat, dog, rabbit, and ape, marks out the 1st thoracic as the common upper limit of the visceral outflow. Of the other observations tending to show the existence of such fibres at higher levels, the latest experimental worker has thrown doubt upon their trustworthiness, on the grounds of insufficient certainty in the enumeration of the nerves, or in the control of the experiments (16, p. 88).

In those cases in which actual dissection has been performed the variations are less wide. Gaskell found the limit in the dog to be the 11nd thoracic, and Langley in cat, rabbit, and dog, at the 1st thoracic root. The latter made a rough count of the fibres medullated in the rami of the 1st thoracic nerve root of the dog, and found about five hundred present (16, p. 116).

2. *The Rami in Man.*

The data at present recorded is very meagre. Suggestions are made in Quain (18) on the analogy of the conditions in the lower animals, that the anterior limit of the white rami is most probably the 1st thoracic nerve.

Two observations bearing somewhat upon the subject are to be found in the remarks on the origin of the great splanchnic nerve. Snow Beck (1, p. 215) notes the origin of tubular fibres for this nerve from all the superior intercostal nerves, and Rüdinger (19) traces the origin of white fibres from the 11nd thoracic root to the same trunk nerve. There appear to be no observations bearing upon the origin of splanchnic fibres for the upper regions.

### 3. *Present Examination—Methods and Scope.*

In this examination into these nerves in the human subject, I have endeavoured to obtain results similar to those obtained in my earlier examinations of the lumbar rami and the pelvic splanchnics, and to those obtained by Langley for the cat, dog, and rabbit.

Foetuses ranging from the eight months (48 cm.) to full time (55 cm.) were used. The subjects were dissected immediately on receipt, in the fresh state; the whole of the cervical and upper thoracic nerves and the sympathetic cord, with the connecting rami, were removed *en masse* to osmic acid (1 per cent. solution) for twenty-four hours, thence into weak alcohol for twelve hours. The nerves and cord were then fixed for the purpose of making a minute dissection of the rami. A part of each ramus was cleaned, its constituent fibres teased out in rows, and the character and number of the white fibres therein ascertained by examination with the microscope. When the number of white fibres was small, as nearly an individual count as possible was made, whilst in rami containing large numbers of the smaller fibres, the number was estimated by the aid of a micro-millimetre eye-piece.

These methods of investigation were employed in six cases, which, from the use of both sides, give twelve plexuses.

Appended are the drawings of the various dissections. To each of these there corresponds an analytical table, giving the results of the examination of each ramus, and from these analyses a general table (III.) has been prepared, which states the form of plexus examined, the number of white fibres found connected with each spinal nerve, and the averages for each spinal nerve from nerve V to XII inclusive.

### 4. *Results.*

From an examination of the analyses of the several dissections, and of the summary of the results given in the general table, it will be seen that medullated fibres were found throughout the range of rami examined, but that the character and number of these fibres is strikingly different when the upper







and lower regions—Vth to VIIIth cervical and Ist to IVth thoracic—are compared.

The white fibres have been separated into two categories, a class for those under  $4\mu$  in diameter, and another for those of a diameter of  $4\mu$  and exceeding it. The significance to be attached to the varying sizes of medullated fibres has been pointed out repeatedly. The matter was briefly summarised in my earliest paper. Observers are in agreement that the small white fibres of a diameter, from  $1.8$  to  $3.6\mu$ , having a characteristic bundle formation, are to be regarded as forming the efferent fibres of the sympathetic system, whilst those of the larger size have been shown by Edgeworth to be afferent in function.

The analyses show that the coarse fibres are scattered throughout the region examined in the same manner as was found in the lumbar region, and the irregular character of the distribution is such that no general plan of their passage through the rami can be formulated.

The distribution of the fibres of the smaller size is, however, one which may be regarded as sharply defined. The analyses show that their numbers were great in the lower rami, and that there was a sudden and marked drop in their numbers, amounting in some cases to a complete cessation, after passing the level of the rami of Ist thoracic nerve. Beyond this level the small white fibres in the rami were in most cases few in number, and scattered throughout the non-medullated fibres—(Table III.).

The exceptions to this manner of distribution are few. In subject 'L,' a case in which the plexuses for both the fore and hind limbs were of the high form, typical bundles of small white fibres were found in the rami connected with the VIIIth cervical nerve, and there could be no doubt that in this case the limit of outflow was extended upwards to include this spinal nerve. Bundles of small fibres were found in the rami of the VIIIth cervical nerve in other cases, and in one case, 'M' right, in the VIIth cervical rami, but in these cases the number of fibres within the bundles and within the rami as a whole, was too small to warrant an upward extension of the limit of efferent outflow so as to include these, when their small numbers were compared with the numbers contained in

the rami of succeeding nerves. The case of 'Q' left is somewhat doubtful, for in each of the two large grey rami connected with the VIIIth cervical nerve there was a bundle of about twenty fibres; in the right side of the same subject there were no such bundles within the rami of the VIIIth cervical nerve; and there was a fall below the general average in the number of fibres within the rami connected with the Ist thoracic nerve, a diminution which may perhaps be considered as consequent on the low form of the limb plexus.

*The conclusion which may be drawn from this examination is that the usual superior limit of the cervico-thoracic visceral efferent nerves in man is at the level of the IXth spinal or Ist thoracic nerve, and that in some few cases the limit may be extended to the VIIIth spinal or VIIIth cervical nerve, and that this variation appears to be connected with the variation in the form of plexus for the fore limb.*

## II.—THE CONDITION OF THE SYMPATHETIC CORD.

### 1. *The Ganglia*—(Table IV.).

The 'typical' plan in which there should be three rami-bearing ganglia in the cervical region, and a ganglion for each nerve in the thoracic region, would appear to be a rare condition, for in these twelve dissections it was only met with once, 'M' left, while even in this case ganglion cells were found to extend along the cord linking the middle and inferior cervical ganglia, showing that the separation of the ganglia was more apparent than real. That linking of ganglia was frequent, can be seen from an examination of Table V., in which an asterisk indicates a continuity of ganglion cells along the cord. In the other cases the ganglia were completely fused to form a lesser number, whilst but rarely the doubling of a ganglion was found.

The only manner in which the superior cervical ganglion was found to vary was in its length. In subject 'L' it was on both sides unusually long, reaching to the level of the transverse process of the Vth cervical vertebra.

A middle ganglion was present nine times; of these it was in one case, 'N' left, double, and in another, 'O' left, the ganglion was constricted to form three parts. In only three of

| Subject. | Sex | Superior Cerv. Gg.                               | Middle Cerv. Gg.                            | Inferior Cerv. Gg.               | 1st Thor. Gg. | 2nd Thor. Gg. | 3rd Thor. Gg. | 4th Thor. Gg. | Annulus.   | Source of Origin of Raml. |                       |                |
|----------|-----|--|---|----------------------------------|---------------|---------------|---------------|---------------|--|---------------------------|-----------------------|----------------|
|          |     |  |   |                                  |               |               |               |               |  | V. Cerv. M.               | VI Cerv.              | VII. Cerv.     |
| L        | R   | Very long, reaches level of Tr. Pca. of V. Cerv. | —   | United                           | +             | +             | +             | +             | Very long. Extends from Sup. to Inf. Cerv. Gang. | Superior gang.            | Superior gang.        | Inferior gang. |
|          | L   | do.  | —   | do.                              | +             | +             | +             | +             | do.  | do.                       | do.                   | do.            |
| M        | R   | +  | + No rami                                   | +                                | +             | +             | +             | +             | —  | do.                       | Inferior              | do.            |
|          | L   | +  | +   | +                                | +             | +             | +             | +             | —  | Middle                    | do.                   | do.            |
| N        | R   | +  | + No rami                                   | +                                | +             | +             | +             | +             | +  | Superior                  | Superior and Inferior | do.            |
|          | L   | +  | + With an extra lower ganglion without rami | United to form Stellate ganglion | +             | +             | +             | +             | +  | Middle                    | Inferior              | do.            |
| O        | R   | +  | + No rami                                   | United to form Stellate ganglion | +             | +             | +             | +             | +  | Superior                  | Superior and Inferior | do.            |
|          | L   | +  | + Triple                                    | do.                              | +             | +             | +             | +             | +  | Middle                    | Middle                | do.            |
| P        | R   | +  | + No rami                                   | United to form Stellate ganglion | +             | Doubled       | +             | +             | +  | Superior                  | Superior              | do.            |
|          | L   | +  | —   | do.                              | United        | +             | +             | +             | —  | do.                       | Inferior              | do.            |
| Q        | R   | +  | + No rami                                   | United to form Stellate ganglion | +             | +             | +             | +             | +  | do.                       | do.                   | do.            |
|          | L   | +  | + No rami                                   | do                               | +             | +             | +             | +             | +  | Inferior                  | do.                   | do.            |

+ indicates present, — absent.

these nine cases, however, did the ganglia give origin to rami communicantes; in the remaining cases it was small, and the reduced ganglion tended to be displaced in a downward direction. The position of the rami for the Vth and VIth cervical nerves in those cases in which no connections with a middle ganglion existed, would appear to show that the ganglion is only partially absorbed into the inferior ganglion, but that some of its ganglion cells are incorporated with the superior ganglion. In the three cases in which a middle ramus-bearing ganglion existed, the ramus of the Vth cervical nerve always sprang from it; in all other cases, excepting one, the ramus sprang from the superior ganglion, or the cords below it, and passed out in a downward direction, whilst the ramus for the VIth cervical nerve arose thrice from the superior ganglion directly or indirectly, twice from superior and inferior, and six times from the inferior ganglion alone.

The tendency towards fusion of the ganglia at the root of the neck is marked. In seven cases a good example of a 'ganglion stellatum' was found, and in three of these the fusion embraced the inferior cervical, first and second thoracic ganglia. Besides these seven cases, in two other, fusion of the inferior cervical and first thoracic ganglia was partial. In a single case the third and fourth thoracic ganglia were fused, and once a third thoracic ganglion was doubled. In three cases, 'N' right, 'P' left, and 'Q' right, small accessory ganglia existed in the cervical region.

## 2. *The Annulus of Vieussens.*

This was present so as to form a complete loop around the subclavian artery in nine cases. In subject 'L' the annulus on each side was abnormally long, extending the whole length between the superior and inferior cervical ganglia.

## 3. *Analysis of the White Fibres in the Sympathetic Cord—* (Table V.).

In ten of the dissections portions of the cord were taken from the links between the ganglia and the portions cleaned and teased out for microscopic examination, in the same manner as

TABLE V.—Analysis of White Fibres in Sympathetic Cord.

| Subject. | Side. | Between Ganglia<br>III. and II.<br>Thoracic. |                     | Between Ganglia<br>II. and I.<br>Thoracic. |                     | Between Ganglia<br>I. Thoracic and<br>Inf. Cerv. |                     | Annulus of Vieussens. |                 |                     |              | Between Ganglia<br>Infer. Cerv. and<br>Mid. Cerv. |                     | Between Ganglia<br>Middle and<br>Superior Cervical. |                 |
|----------|-------|--|---------------------|--|---------------------|--|---------------------|-----------------------|-----------------|---------------------|--------------|---|---------------------|---|-----------------|
|          |       | Under<br>4μ.                                 | 4μ and<br>over.     | Under<br>4μ.                               | 4μ and<br>over.     | Under<br>4μ.                                     | 4μ and<br>over.     | Anterior Limb.        |                 | Posterior Limb.     |              | Under<br>4μ.                                      | 4μ and<br>over.     | Under<br>4μ.  | 4μ and<br>over. |
|          |       | $\frac{1}{2}$<br>mm                          | $\frac{1}{2}$<br>mm | $\frac{1}{2}$<br>mm                        | $\frac{1}{2}$<br>mm | $\frac{1}{2}$<br>mm                              | $\frac{1}{2}$<br>mm | Under<br>4μ.          | 4μ and<br>over. | $\frac{1}{2}$<br>mm | Under<br>4μ. | 4μ and<br>over.                                   | $\frac{1}{2}$<br>mm | Under<br>4μ.  | 4μ and<br>over. |
| M        | R     | —  | — <sup>1</sup>      | b  | 210                 | 15*  | 55*                 | —                     | —               | —                   | —            | 25  | 16                  | 22  | 35              |
|          | L     | —  | — <sup>1</sup>      | b  | 250                 | 20*  | 30*                 | —                     | —               | —                   | —            | 35  | 0*                  | 15  | 0               |
| N        | R     | —  | — <sup>1</sup>      | b  | *                   | *  | *                   | 0                     | 0               | d'                  | 1            | 2   | —                   | 22  | 17              |
|          | L     | 350  | 40                  | b  | *                   | *  | *                   | 0                     | 0               | d''                 | 30           | 5   | —                   | 15  | 20              |
| O        | R     | 300  | 10                  | b  | *                   | *  | *                   | 4                     | 6               | d''                 | 7            | 10  | —                   | 15  | 14              |
|          | L     | 250  | 40                  | b  | 175                 | 22*  | *                   | 6                     | 17              | d''                 | 2            | 5*  | —                   | 4   | 14              |
| P        | R     | —  | — <sup>1</sup>      | b  | *                   | *  | *                   | —                     | — <sup>1</sup>  | d'                  | —            | — <sup>1</sup>                                    | —                   | — <sup>1</sup>                                      | — <sup>1</sup>  |
|          | L     | 200  | 40                  | b  | *                   | *  | *                   | —                     | —               | —                   | —            | —   | *                   | 21  | 22              |
| Q        | R     | 370  | 40                  | b  | 140                 | 5  | *                   | 0                     | 0               | d''                 | 10           | 6   | —                   | 0   | 13              |
|          | L     | 300  | 32                  | b  | 190                 | 37   | *                   | 10                    | 5               | d''                 | 0            | 15  | —                   | 5   | 21              |

<sup>1</sup> The fibres were not counted in these sections.

\* Indicates continuity of ganglion cells in cord.

employed for the rami communicantes, with a view to ascertaining the condition of the white fibres within the cord.

In many cases, indicated in the table by an asterisk, no count of the fibres could be made, owing to the presence of numerous ganglion cells which united the contiguous ganglia.

The fibres were found to bear the same characters as those in the rami, the small white fibres were very numerous in the thoracic portion of the cord, and their numbers rapidly diminished in the upper sections. The coarser fibres were pretty evenly scattered throughout the cord.

### III.—THE PLAN OF THE RAMI COMMUNICANTES.

In the thoracic region a very uniform plan of arrangement was found to exist. In most cases each spinal nerve had connected with it three rami. The most anterior was a slender ramus, composed of almost wholly small white fibres, which passed from the spinal nerve obliquely upwards across the head of the rib to the ganglion of the nerve above. This ramus is a very delicate one, and liable to be missed unless special care be taken. Connecting the nerve and its own proper ganglion were two rami, which may be distinctly separate at the first fresh dissection. Of these the upper usually proves to contain a large number of the small white fibres, and the lower to be mostly grey fibres.

In some cases the separation of the two parts of the double connection was only distinguished after the staining with osmic acid; in these cases the rami are lettered as one in the figure, and an indication of the double nature made in the analysis. In yet other cases the parts are so firmly united as to constitute only one ramus.

In the upper region of the thoracic cord, the distinction of white and grey rami are fairly sharply maintained. The extreme shortness of these upper thoracic rami must be emphasised.

As regards the rami connected with the cervical nerves, they are variable in number, and in their connections with cord or ganglia. The rami of the first three cervical nerves almost



always sprang from the superior cervical ganglion, that of the IVth cervical nerve from the cord immediately below this ganglion. In one case, 'M' left, the rami of the IIIrd and IVth nerves sprang from a middle ganglion.

The origin of the rami for nerves V and VI has been discussed, and is shown in Table IV.

For nerves VII and VIII there are usually two rami to each nerve, which always spring from an inferior cervical or stellate ganglion.

#### IV.—THE FORM OF PLEXUS.

I have used for the classification of the forms of plexuses found, the size of the communication from the IVth to the Vth cervical nerve, and the size and nerve of origin of the intercosto-humeral nerve.

The cases, which were labelled and dissected immediately on receipt through a period of ten months, form a complete series from high to very low forms of plexuses. It may be noted also, that the medium and low forms are the most numerous, and that the extreme forms are in the direction of a downward shifting of the limb plexus; this is in striking contrast to the forms of plexuses dissected in the examination of the lumbar rami and the pelvic splanchnics, where the majority were medium and high, and the extreme forms were those showing an upward shifting of the plexus. These conditions may very well be viewed in connection with the theory of the tendency to the diminution of the extent of the trunk both from below and above.

The plexuses of subject 'Q' are so much out of the ordinary range that some extra details of their arrangements may be given. It appears they form the greatest downward shifting yet recorded (Table VI.).

The plexuses are remarkable in the loss of supply to the limbs from the IVth and partly the Vth cervical nerves, which is compensated for by the absorption of the greater part of the IIInd thoracic nerve into the plexus. This supply passed upwards within the thorax across the head of the second rib and the neck of the first rib to join the Ist thoracic nerve on the upper

TABLE VI.—*Forms of Plexuses in Subject 'Q.'*

| Nerves.  | Right Side.  | Left Side.   |
|--|--|--|
| <b><i>Cervical Plexus:—</i></b><br>Com. fr. Cerv. Nerve to XIIth Cranial.<br>Descendens Cervicis.<br>Communicans do.<br>Phrenic Nerve.   | Small communication from I Cervical only.<br>Very small, from I Cerv. only.<br>From II and III Cerv.<br>No Ansa.<br>IV and V Cerv., Branch from IV slightly larger.  | Same.<br>Same.<br>Same.<br>IV and V in equal proportions. They do not unite until within thorax.   |
| <b><i>Brachial Plexus:—</i></b><br>Com. fr. IV to V Cerv.<br>Supply to plexus fr. IIInd Dorsal.<br>Musculo-cutaneous.<br>Median:—Outer Head.<br>Inner Head.<br>Ulnar.<br>Internal cutaneous.<br>Lesser do.<br>Musculo-spiral.<br>Circumflex.<br>Intercosto-humeral:—<br>From II Dorsal.<br>III do.<br>IV do. | Absent.<br>Two-thirds whole root.<br>V <sub>(2)</sub> VI <sub>(3)</sub><br>V <sub>(1)</sub> VI <sub>(1)</sub> VII <sub>(7)</sub><br>VII <sub>(1)</sub> VIII <sub>(6)</sub> I <sub>(6)</sub> II <sub>(1)</sub><br>VIII <sub>(6)</sub> I <sub>(8)</sub> II <sub>(1)</sub><br>I <sub>(2)</sub> II <sub>(3)</sub><br>II <sub>(1)</sub><br>V <sub>(2)</sub> VI <sub>(10)</sub> VII <sub>(10)</sub> VIII <sub>(11)</sub><br>I <sub>(3)</sub><br>V <sub>(5)</sub> VI <sub>(7)</sub> VII <sub>(5)</sub> VIII <sub>(3)</sub><br>I <sub>(1)</sub><br>One-third Second Intercostal, joins with lesser internal cutaneous twig.<br>Two-thirds Third Intercostal, descends alone to near elbow.<br>Not present. | Extremely minute.<br>Two-thirds whole root.<br>V <sub>(2)</sub> VI <sub>(3)</sub><br>VI <sub>(2)</sub> VII <sub>(6)</sub><br>VII <sub>(2)</sub> VIII <sub>(10)</sub> I <sub>(3)</sub> II <sub>(1)</sub><br>VIII <sub>(5)</sub> I <sub>(7)</sub> II <sub>(2)</sub><br>I <sub>(2)</sub> II <sub>(3)</sub><br>II <sub>(1)</sub><br>V <sub>(1)</sub> VI <sub>(7)</sub> VII <sub>(14)</sub> VIII <sub>(8)</sub><br>I <sub>(2)</sub><br>V <sub>(6)</sub> VI <sub>(8)</sub> VII <sub>(3)</sub> VIII <sub>(1)</sub><br>One-half Second Intercostal, joins with lesser internal cutaneous twig.<br>Two-thirds Third Intercostal, ends middle third of arm.<br>One-half Fourth Intercostal, ends upper third of arm. |
| <b><i>Lumbo-sacral Plexus:—</i></b><br>Com. fr. XII Dor. to I L.<br>Nv. Furcalis.  | Absent.<br>Com. from IV. L. very minute.   | Absent.<br>No com. fr. IV. Lumb. Ant. Crural arises from V. L.   |

The small bracketed letters indicated the approximate proportion of the contributions of the plexus roots to the nerves.

surface of the neck of this rib. The pressure exerted by the sharp bend which these nerves make over the bone might be supposed to be capable of exerting an influence injurious to the growth of the rib; in this case, however, no sign of grooving or defect of nutrition could be discerned. These conditions may be compared with those found by Lane (15, p. 267) in an adult subject, in which, with considerable coincident changes in the skeleton, the IXth nerve "was joined by a large branch of the Xth spinal nerve."

In this subject the conditions of the other plexuses or plexiform connections of the spinal nerves were examined, with the interesting result that the outflow of the spinal nerves in their relation to the column was found to be shifted *en masse* in a caudal direction. The communication from the spinal nerves to the XIIth cranial was from the Ist cervical only, the descendens cervicis derived therefrom was very slender, and was successively augmented by communications from the IIInd and IIIrd nerves. There was no loop formed, but merely a multiple origin of a single nerve, which terminated in branches of supply (fig. 12) to the depressors of the hyoid bone. The origin of the phrenic nerve was also depressed, being in both cases only from the IVth and Vth nerves, and on the right side from these nerves in equal proportions. The two branches from these sources ran a separate course in the neck, only uniting within the thorax (*cf.* W. Turner, 22, p. 102).<sup>1</sup>

In the lumbo-sacral region there was found to be no communication from the XIIth thoracic to the Ist lumbar, and on one side all the IVth lumbar was used within the lumbar plexus, and the anterior crural nerve derived a considerable branch from the Vth lumbar nerve.

In the large extent in which the IIInd thoracic nerve enters into the formation of the fore-limb plexus, this case resembles the conditions found in lower animals, *e.g.*, cat and ape. It would have been a matter of considerable interest if the contribution which the IIInd thoracic nerve made to the ulnar and median nerves could have been traced out to its peripheral distribution

<sup>1</sup> I have since seen two cases of delayed union of the origins of the phrenic in adults. In each of these the contribution from the fifth nerve passed superficially to the subclavian vein.

and compared with the distribution of this connection in the *Macacus rhesus*, as given by Sherrington (21, p. 741); but this could not be done here, as it would have endangered the safety of the rami communicantes, the white fibres of which break up very early.

There was no abnormality in the arrangements of the ribs, nor yet in the vertebral column.

It is of considerable interest to compare these observations with those of cases 'L,' 'M,' and 'N,' where the brachial and lumbo-sacral plexuses were examined.

In 'L' the plexuses are 'high' forms throughout; in 'M' 'medium' fore-limb and 'low' hind-limb plexuses, and in 'N' 'medium' fore-limb and 'high' hind-limb plexuses are associated together.

The plexuses of 'L' and 'Q' show a shifting *en masse* of the nerves in an upward and downward direction respectively, whilst 'M' shows an expansion from the downward shifting of the hind-limb plexuses, and 'N' a compression from the upward displacement of the same plexuses, whilst both possess the 'medium' form of fore-limb plexuses.

In 'Q' the shifting was ascertained to extend to the upper cervical region as well as to the limb plexuses.

#### V.—AN INTER-THORACIC COMMUNICATION FROM THE IIND TO 1ST THORACIC NERVE.

This communication was present in seven out of the twelve dissections (including 'Q'); this is a rather smaller proportion than that given by Cunningham (6) from his dissections, but the occurrence is more frequent than that indicated by Herringham (14), who says the communication is too small to be observed in foetal dissections.

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## INDEX TO FIGURES.

Roman numerals—Spinal and Cranial nerve roots.

Arabic numerals—Rami communicantes.

Roman letters *a* to *e*—Sections of Sympathetic cord.

*c.c.*—Communicans cervicis.

*d.c.*—Descendens cervicis.

*d.h.*—Branches to depressor muscles of hyoid bone.

*m.h.*—Branches to m. genio-hyoideus and thyro-hyoideus.

*i.h.*—Intercosto-humeral nerve.

*ph.*—Phrenic nerve.

Greek characters—Branches of distribution of the Sympathetic.

$\theta$ —Thyroid branches.

$\kappa$ —Cardiac nerves.

$\lambda$ —Twigs to column, ligaments, and aorta.

$\pi$ —Pulmonary branches.

*s*—Do. along subclavian artery.

*v*—Do. along vertebral artery.

## Analysis.

L. right, ♂, 55 cm.

| Nerve Root.  | Ramus. | No. of White Fibres. |                      | Description.  |
|--------------|--------|----------------------|----------------------|---|
|              |        | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |   |
| V Cervical   | 1      | 0                    | 1                    | Large grey ramus.   |
| VI "         | 2      | 0                    | 6                    | do.   |
| VII "        | 3      | 0                    | 10                   | do.   |
| VIII "       | 4      | 45                   | 3                    | Large grey ramus, white<br>fibres in two bundles of<br>20 each. |
| " "          | 5      | 0                    | 0                    | Large grey ramus.   |
| " I Thoracic | 6      | 75                   | 25                   | Many grey fibres.   |
| I "          | 7      | 85                   | 10                   | Very large grey ramus.  |
| II "         | 8      | ...                  | ...                  | Many grey fibres.   |
| " "          | 9      | 45                   | 5                    | do.   |
| III "        | 10     | 120                  | 13                   | Nearly all white.   |
| " "          | 11     | 110                  | 32                   | $\frac{2}{3}$ grey.   |
| IV "         | 12     | 230                  | 16                   | Most white, few grey.   |
| " "          | 13     | 170                  | 43                   | $\frac{2}{3}$ grey.   |

## Analysis.

L. left, ♂, 55 cm.

| Nerve Root. | Ramus. | No. of White Fibres. |                      | Description.   |
|-------------|--------|----------------------|----------------------|--|
|             |        | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical  | 1      | ...                  | ...                  | ...  |
| VI "        | 2      | ...                  | ...                  | ...  |
| VII "       | 3      | 0                    | 6                    | Very large grey ramus.   |
| VIII "      | 4      | 45                   | 8                    | Very large grey ramus,<br>white fibres in one bundle<br>of 40. |
| " "         | 5      | 25                   | 2                    | Very large grey ramus,<br>white fibres in one bundle<br>of 20. |
| " "         | 5      | 25                   | 2                    | Very large grey ramus,<br>white fibres in one bundle<br>of 20. |
| I Thoracic  | 6      | 85                   | 3                    | ...  |
| II "        | 7      | 75                   | 5                    | White ramus, with $\frac{1}{4}$ grey.                          |
| " "         | 8      | 240                  | 70                   | $\frac{2}{3}$ grey fibres.                                     |
| " "         | 9      | 60                   | 10                   | Large grey ramus.  |
| III "       | 10     | 80                   | 5                    | White, some grey.  |
| " "         | 11     | 80                   | 50                   | $\frac{2}{3}$ grey.  |
| IV "        | 12     | ...                  | ...                  | Lost, fine white ramus.  |
| " "         | 13     | 200                  | 55                   | $\frac{2}{3}$ white.   |

Analysis.

M. ♀, 54 cm. right side.

| Nerve Root.  | Ramus.            | No. of White Fibres. |                      | Description.                                     |
|--------------|-------------------|----------------------|----------------------|--|
|              |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical   | 1                 | 0                    | 5                    | Grey ramus.                                      |
| VI "         | 2                 | 5                    | 20                   | Large do.  |
| VII "        | 3                 | 2                    | 8                    | do.  |
| " "          | 4                 | 12                   | 6                    | Very large ramus. White<br>fibres in one bundle. |
| VIII "       | 5                 | 4                    | 1                    | Small grey ramus.                                |
| " "          | 6                 | 5                    | 0                    | Very large grey ramus.                           |
| " I Thoracic | 7                 | 8                    | 0                    | Small grey ramus.                                |
| " "          | 8                 | 40                   | 2                    | Large do.  |
| " "          | 9                 | 70                   | 1                    | Many grey fibres.                                |
| II "         | 10                | 240                  | 35                   | do.  |
| " "          | 11                | 70                   | 3                    | Large grey ramus.                                |
| III "        | 12                | 30                   | 4                    | Many grey fibres.                                |
| " "          | 13 <sup>(2)</sup> | 115                  | 13                   | Very do.   |
| IV "         | 14                | 140                  | 6                    | Few grey fibres.                                 |
| " "          | 15 <sup>a</sup>   | 400                  | 10                   | do.  |
| " "          | b                 | 30                   | 7                    | Large grey ramus.                                |

Analysis.

M. ♀, 54 cm. left side.

| Nerve Root.  | Ramus.            | No. of White Fibres. |                      | Description.                         |
|--------------|-------------------|----------------------|----------------------|--------------------------------------|
|              |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |                                      |
| V Cervical   | 1                 | 0                    | 6                    | Grey ramus.                          |
| VI "         | 2                 | 0                    | 0                    | Very large grey ramus.               |
| VII "        | 3                 | 0                    | 0                    | Small grey ramus.                    |
| " "          | 4                 | 0                    | 0                    | Large grey ramus.                    |
| VIII "       | 5                 | 0                    | 5                    | do.                                  |
| " I Thoracic | 6                 | 10                   | 25                   | do.                                  |
| " "          | 7                 | 40                   | 0                    | do.                                  |
| II "         | 8                 | 135                  | 40                   | White ramus but many grey<br>fibres. |
| " "          | 9                 | 110                  | 15                   | 3 grey.                              |
| III "        | 10                | 45                   | 3                    | Small white ramus.                   |
| " "          | 11 <sup>(2)</sup> | 300                  | 50                   | 3 grey.                              |
| IV "         | 12                | ...                  | ...                  | White ramus, lost.                   |
| " "          | 13 <sup>(2)</sup> | 175                  | 10                   | Many grey fibres.                    |



Analysis.  
N. right, ♂, 53 cm.

| Nerve Root. | Ramus.            | No. of White Fibres. |                      | Description.   |
|-------------|-------------------|----------------------|----------------------|--|
|             |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical  | 1                 | 0                    | 0                    | Grey ramus.  |
| VI "        | 2                 | 0                    | 0                    | Large do.  |
| VII "       | 3                 | 0                    | 5                    | Grey ramus.  |
| VII "       | 4                 | 0                    | 20                   | Large do.  |
| " "         | 5                 | 0                    | 8                    | Grey ramus.  |
| VIII "      | 6                 | 0                    | 4                    | do.  |
| VIII "      | 7                 | 0                    | 5                    | Large grey ramus.                                      |
| " "         | 8                 | 0                    | 1                    | Medium grey ramus.                                     |
| " "         | 9                 | 20                   | 5                    | Grey ramus, white fibres in<br>two bundles of 10 each. |
| I Thoracic  | 10                | 120                  | 5                    | $\frac{1}{2}$ grey.                                    |
| " "         | 11                | 150                  | 2                    | $\frac{1}{2}$ do.                                      |
| II "        | 12                | 210                  | 17                   | $\frac{1}{2}$ do.                                      |
| " "         | 13                | 0                    | 0                    | All grey.  |
| III "       | 14                | 80                   | 8                    | $\frac{1}{2}$ do.                                      |
| " "         | 15                | 230                  | 9                    | $\frac{1}{2}$ do.                                      |
| " "         | 16                | 30                   | 2                    | Mostly grey.   |
| IV "        | 17                | 90                   | 1                    | Few grey.  |
| " "         | 18 <sup>(2)</sup> | 20                   | 15                   | Large grey.  |

Analysis.  
N. left, ♂, 53 cm.

| Nerve Root.  | Ramus. | No. of White Fibres. |                      | Description.                                 |
|--------------|--------|----------------------|----------------------|--|
|              |        | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical   | 1      | 0                    | 25                   | Small grey ramus.                            |
| " "          | 2      | 0                    | 0                    | do.  |
| VI "         | 3      | 0                    | 0                    | do.  |
| VII "        | 4      | 0                    | 6                    | Very large grey ramus.                       |
| VIII "       | 5      | 20                   | 10                   | Large grey ramus, white<br>fibres scattered. |
| " "          | 6      | 0                    | 6                    | Grey ramus.                                  |
| " I Thoracic | 7      | 60                   | 20                   | Many grey fibres.                            |
| " "          | 8      | 75                   | 25                   | do.  |
| " "          | 9      | 10                   | 0                    | Large grey ramus.                            |
| II "         | 10     | 80                   | 15                   | Small white.                                 |
| " "          | 11a    | 100                  | 8                    | } Very many grey.                            |
| " "          | b      | 5                    | 0                    |  |
| III "        | 12     | 35                   | 10                   | Many grey.                                   |
| " "          | 13a    | 150                  | 6                    | $\frac{2}{3}$ grey.                          |
| " "          | b      | 20                   | 0                    | Large grey ramus.                            |
| IV "         | 14     | 100                  | 5                    | White, few grey.                             |
| " "          | 15     | 70                   | 10                   | Large grey ramus.                            |

Analysis.  
O. right, ♂, 48 cm.

| Nerve Root.  | Ramus.            | No. of White Fibres. |                      | Description.   |
|--------------|-------------------|----------------------|----------------------|--|
|              |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical   | 1                 | 0                    | 7                    | Medium grey ramus.                                       |
| VI "         | 2                 | 0                    | 0                    | Grey ramus.  |
| VII "        | 3                 | 15                   | 2                    | Very large grey ramus,<br>white fibres in one<br>bundle. |
| VIII "       | 4                 | 0                    | 0                    | Small grey.  |
|              | 5                 | 0                    | 0                    | do.  |
|              | 6 <sub>(3)</sub>  | 10                   | 3                    | Very large grey ramus.                                   |
| " I Thoracic | 7                 | 65                   | 5                    | $\frac{3}{4}$ grey.                                      |
| " "          | 8                 | 90                   | 5                    | Most grey.   |
| " "          | 9                 | 0                    | 0                    | Very small grey.   |
| " "          | 10                | 0                    | 0                    | do.  |
| " "          | 11                | 0                    | 0                    | do.  |
| II "         | 12                | 70                   | 10                   | $\frac{1}{2}$ grey.                                      |
| III "        | 13 <sub>(2)</sub> | 65                   | 4                    | Large grey ramus.  |
|              | 14                | 100                  | 20                   | Few grey fibres.   |
| " "          | 15                | 60                   | 0                    | Large grey ramus.  |
| " "          | 16                | 130                  | 6                    | $\frac{1}{2}$ grey.                                      |
| IV "         | 17                | 40                   | 1                    | Few grey.  |
| " "          | 18                | 15                   | 3                    | Large grey.  |
| " "          | 19                | 150                  | 8                    | Medium.  |

Analysis.  
O. left, ♂, 48 cm.

| Nerve Root.  | Ramus.            | No. of White Fibres. |                      | Description.                                    |
|--------------|-------------------|----------------------|----------------------|---|
|              |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |   |
| V Cervical   | 1                 | 0                    | 2                    | Grey ramus.                                     |
| VI "         | 2                 | ...                  | ...                  | Lost.   |
| VII "        | 3                 | 0                    | 4                    | Very large grey ramus.                          |
| VIII "       | 4                 | 0                    | 10                   | Medium grey ramus.                              |
|              | 5                 | 3                    | 7                    | Large grey ramus.                               |
| " "          | 6                 | 14                   | 3                    | Grey ramus, white fibres in<br>one bundle of 8. |
| " I Thoracic | 7                 | 2                    | 0                    | Grey ramus.                                     |
|              | 8                 | 95                   | 20                   | $\frac{1}{2}$ grey.                             |
|              | 9                 | 70                   | 10                   | do.   |
| " "          | 10                | 35                   | 2                    | $\frac{3}{4}$ do.                               |
| II "         | 11                | 200                  | 11                   | Few do.   |
| " "          | 12                | 120                  | 20                   | do.   |
| " "          | 13                | 20                   | 0                    | $\frac{3}{4}$ do.                               |
| III "        | 14                | 160                  | 10                   | Few do.   |
| " "          | 15 <sub>(2)</sub> | 0                    | 0                    | Large grey ramus.                               |
| IV "         | 16                | 80                   | 0                    | Few grey.                                       |
| " "          | 17                | 200                  | 10                   | $\frac{1}{2}$ do.                               |
| " "          | 18                | 20                   | 0                    | Large grey ramus.                               |

Analysis.  
P. right, ♂, 52.5 cm.

| Nerve Root. | Ramus.            | No. of White Fibres. |                      | Description.           |
|-------------|-------------------|----------------------|----------------------|------------------------|
|             |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |                        |
| V Cervical  | 1                 | 5                    | 30                   | Grey ramus.            |
| VI "        | 2                 | 2                    | 1                    | Large do.              |
| VII "       | 3                 | 0                    | 2                    | Very large ramus.      |
| VIII "      | 4                 | 1                    | 0                    | Grey ramus.            |
| " "         | 5                 | 4                    | 0                    | Very large do.         |
| " "         | 6                 | 0                    | 1                    | Large grey do.         |
| I Thoracic  | 7                 | 60                   | 20                   | $\frac{1}{2}$ grey.    |
| " "         | 8                 | 0                    | 2                    | Very large grey ramus. |
| " "         | 9                 | 30                   | 5                    | $\frac{1}{2}$ grey.    |
| II "        | 10                | 140                  | 12                   | $\frac{1}{2}$ grey.    |
| " "         | 11                | 150                  | 20                   | do.                    |
| " "         | 12                | 20                   | 0                    | Large grey ramus.      |
| III "       | 13                | 110                  | 9                    | $\frac{1}{2}$ grey.    |
| " "         | 14 <sup>(2)</sup> | 20                   | 0                    | Large grey ramus.      |
| IV "        | 15                | 70                   | 0                    | Few grey fibres.       |
| " "         | 16                | 100                  | 10                   | Very many do.          |
| " "         | 17                | 50                   | 3                    | do.                    |

Analysis.  
P. left, ♂, 52.5 cm.

| Nerve Root. | Ramus. | No. of White Fibres. |                      | Description.   |
|-------------|--------|----------------------|----------------------|--|
|             |        | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |  |
| V Cervical  | 1      | 0                    | 0                    | With this ramus there runs a muscular branch of 100 fibres of 3-4 $\mu$ , past the accessory ganglion. |
| VI "        | 2      | 0                    | 0                    |  |
| VII "       | 3      | 20                   | 8                    | Large grey ramus, white fibres scattered.  |
| VIII "      | 4      | 30                   | 20                   | Very large grey ramus, white fibres scattered.   |
| " "         | 5      | 0                    | 0                    | Grey ramus.  |
| I Thoracic  | 6      | 140                  | 10                   | Few grey fibres.   |
| " "         | 7      | 0                    | 0                    | Large grey ramus.  |
| II "        | 8      | 40                   | 0                    | Few grey fibres.   |
| " "         | 9      | 200                  | 13                   | $\frac{1}{2}$ grey.  |
| III "       | 10     | 140                  | 4                    | White ramus, some grey.  |
| " "         | 11     | 0                    | 4                    | Grey ramus.  |
| IV "        | 12     | 150                  | 0                    | Few grey fibres.   |
| " "         | 13     | 80                   | 30                   | Many do.   |
| " "         | 14     | 0                    | 10                   | Grey ramus.  |

## Analysis.

Q. right, ♂, 54 cm. (14 days extra-uterine).

| Nerve Root. | Ramus.           | No. of White Fibres. |                      | Description.               |
|-------------|------------------|----------------------|----------------------|----------------------------|
|             |                  | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |                            |
| V Cervical  | 1                | 0                    | 0                    | Small grey ramus.          |
| VI "        | 2                | 8                    | 2                    | Large grey do.             |
| VII "       | 3 <sup>(2)</sup> | 10                   | 0                    | do. white scattered.       |
| VIII "      | 4                | 20                   | 10                   | do.                        |
| I Thoracic  | 5                | 90                   | 5                    | $\frac{3}{4}$ grey.        |
| II "        | 6                | 85                   | 6                    | do.                        |
| " "         | 7                | 80                   | 5                    | Nearly all white.          |
| " "         | 8                | 240                  | 9                    | $\frac{1}{2}$ grey fibres. |
| " "         | 9                | 20                   | 0                    | Mostly grey ramus.         |
| III "       | 10               | ...                  | ...                  | Small white ramus—lost.    |
| " "         | 11               | 310                  | 6                    | Few grey fibres.           |
| " "         | 12               | 0                    | 9                    | Grey ramus.                |
| IV "        | 13               | 65                   | 0                    | Nearly all white.          |
| " "         | 14               | 60                   | 0                    | $\frac{3}{4}$ grey.        |

## Analysis.

Q. left, ♂, 54 cm. (14 days extra-uterine).

| Nerve Root. | Ramus.            | No. of White Fibres. |                      | Description.  |
|-------------|-------------------|----------------------|----------------------|---|
|             |                   | Under<br>4 $\mu$ .   | 4 $\mu$ and<br>over. |   |
| V Cervical  | 1                 | 20                   | 10                   | Large grey ramus, with scattered white.             |
| VI "        | 2                 | 5                    | 10                   | Grey ramus.   |
| VII "       | 3                 | 8                    | 2                    | Large grey ramus.                                   |
| " "         | 4                 | 30                   | 3                    | do. white scattered.                                |
| VIII "      | 5                 | 23                   | 7                    | Large grey ramus, white fibres in one bundle of 20. |
| " "         | 6                 | 20                   | 4                    | Large grey ramus, white fibres in one bundle of 20. |
| I Thoracic  | 7                 | 80                   | 1                    | Nearly all white.                                   |
| " "         | 8 <sup>(2)</sup>  | 70                   | 5                    | Large grey ramus.                                   |
| II "        | 9                 | 170                  | 4                    | Nearly all white.                                   |
| " "         | 10 <sup>(2)</sup> | 150                  | 20                   | $\frac{3}{4}$ grey fibres.                          |
| III "       | 11                | 70                   | 3                    | Nearly all white.                                   |
| " "         | 12 <sup>(2)</sup> | 300                  | 40                   | $\frac{1}{2}$ grey fibres.                          |
| IV "        | 13                | 100                  | 0                    | Nearly all white.                                   |
| " "         | 14                | 220                  | 2                    | $\frac{3}{4}$ grey fibres.                          |

FIG. 1.—Subject, 'L,' right side.  
(♂ 55 c.m.)

FIG. 2.—Subject, 'L,' left side.  
(♂ 55 c.m.)

N. B. H., *del.*



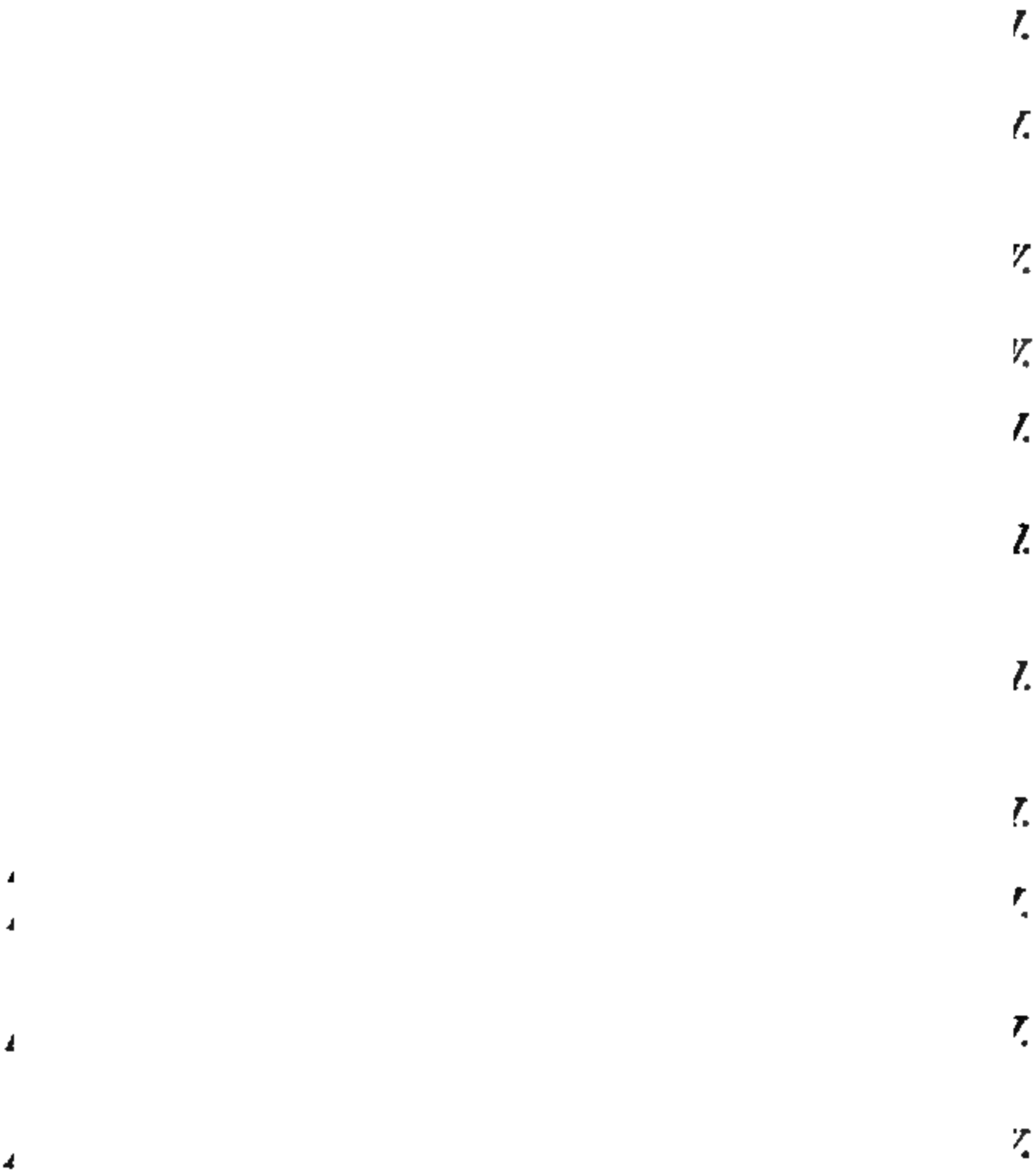


FIG. 3.—Subject, 'M,' right side.  
(♀ 54 c.m.)

FIG. 4.—Subject, 'M,' left side.  
(♀ 54 c.m.)

N. B. H., *del.*





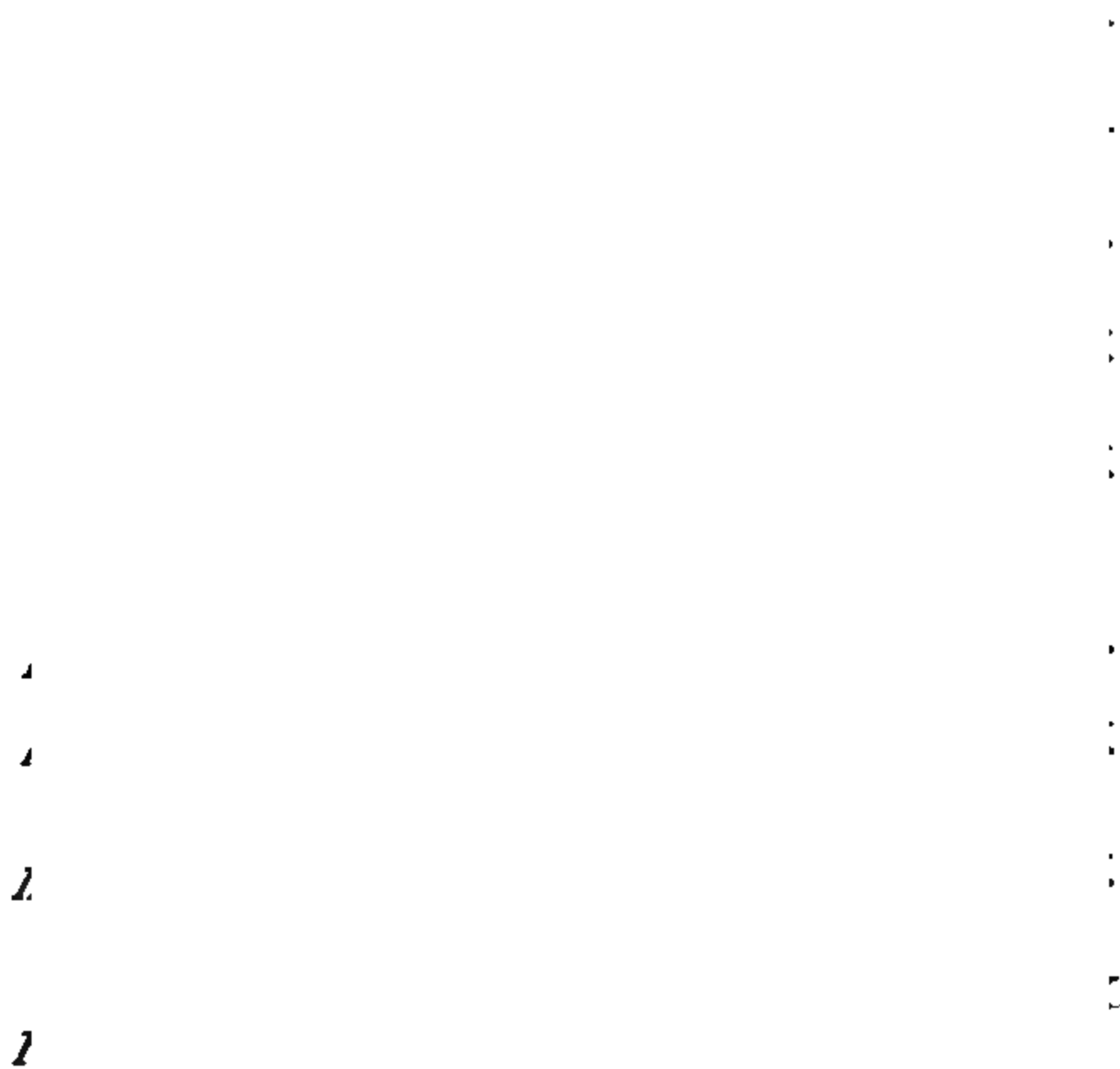


FIG. 5.—Subject, 'N,' right side.  
(♂ 53 c.m.)

FIG. 6. —Subject, 'N,' left side.  
(♂ 53 c.m.)

N. B. H., *del.*



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I.  
I.  
  
II.  
  
D

FIG. 7.—Subject, 'O,' right side.  
(♂ 48 c.m.)

FIG. 8.—Subject, 'O,' left side.  
(♂ 48 c.m.)

N. B. H., *del.*



1

1

1

1

FIG. 9.—Subject, 'P,' right side.  
(♂ 52.5 c.m.)

FIG. 10.—Subject, 'P,' left side.  
(♂ 52.5 c.m.)

N. B. H., *del.*



*I.*

*L*

*L*

*I*

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*I*

*I*

FIG. 11.—Subject, 'Q,' right side. (♂ 54 c.m.)  
Very low form of plexus, see page 370, Table VI.

FIG. 12.—Subject, 'Q,' left side. (♂ 54 c.m.)  
Very low form of plexus, see page 370, Table VI.

N. B. H. *del.*





THE MINUTE STRUCTURE OF THE MEDULLARY SHEATH OF NERVE-FIBRES. By WILLIAM H. WYNN, B.Sc. (Lond.), *Gold Medallist in Physiology, Lond. Univ.; Heslop and Constance Naden Gold Medallist, Mason University College, Birmingham.* (PLATES L, LI.)

(*From the Physiological Laboratory, Mason University College, Birmingham.*)

IN this paper I purpose describing the result of an investigation on the medullary sheath in which the improved methods of hardening and staining nervous tissues, especially by the recent modifications of the Weigert-Pal method, have been employed. The appearances met with have not previously been described, and from their constancy and regularity are of great interest.

But before entering upon the more original observations, it is perhaps desirable to give a brief *résumé* of our present knowledge of the histology of the medullary sheath, so far as it concerns this paper.

All observers are agreed that the sheath consists of two parts—the fatty substance, or myelin, and a supporting framework or stroma. It is concerning the nature and structure of the latter that there is a great diversity of opinion among histologists. Many isolated observations have been recorded, but as yet no theory has been constructed which affords an adequate explanation of them.

*Ranvier*, who first described the original protoplasmic condition of the sheath, considers that the protoplasm has disappeared and become replaced by myelin, except immediately beneath the primitive sheath and immediately surrounding the axis-cylinder, where thin layers still remain. He further considers that these layers are connected by oblique protoplasmic septa corresponding in position to the clefts described by Schmidt, Lantermann, and others, and dividing the sheath up into small conico-cylindrical segments. If the fibres be examined carefully in the fresh condition, the clefts seem to be bridged across by oblique fibres passing from one segment to the other. These fibres are the optical sections of oblique lamellæ passing across the clefts.

*Rezzonico*<sup>1</sup> and *Golgi*,<sup>2</sup> from the examination of fibres treated by a mixture of bichromate of potash and osmic acid, and afterwards by nitrate of silver, find that each cleft is occupied by what appears to be a thread of darkly-stained substance passing spirally around the fibre. They consider that the supporting framework of the sheath consists of a chain of funnels surrounding the axis-cylinder, each funnel being formed by a spiral thread.

A reticular structure pervading the medullary sheath has been described by many observers.

*Ewald* and *Kühne*,<sup>3</sup> by dissolving out the myelin by placing a nerve in strong alcohol, obtained a network readily stained by most dyes. This they considered chemically to be of a horny nature on account of its great resistance to reagents, and especially to gastric and tryptic digestive fluids. Hence it is termed the neuro-keratin network or horny reticulum. This network they regarded as double, one part closely surrounding the axis-cylinder, the other being immediately beneath the primitive sheath.

*Rumpf*<sup>4</sup> agrees with *Ewald* and *Kühne* in the existence of two reticular sheaths with myelin between. He believes that it is narrowed but not interrupted at the nodes of Ranvier, and that there is an albuminoid substance in these sheaths which can be digested with trypsin, leaving behind neuro-keratin; and a cement substance which may be responsible for the slits of Lantermann.

*Tizzoni*<sup>5</sup> believes that there is but one network closely investing the axis-cylinder, and that it is in connection with the slits of Lantermann.

*Koch*<sup>6</sup> also denies the existence of an outer sheath.

*Fleming*<sup>7</sup> believes that the neuro-keratin network is due to the spiral threads of Golgi's funnels, often much twisted, and that there

<sup>1</sup> *Rezzonico*, "Sulla struttura delle fibre nervose del midollo spinale," *Arch. per le Sc. med. Torino*, 1880, iv. 78-90. "Sulla struttura delle fibre nervose del midollo spinale," *Gazz. med. ital. lomb. Milano*, 1879, 8 s., i. 341.

<sup>2</sup> *Golgi*, "Sulla struttura delle fibre nervose midollate periferiche e centrali," *Arch. per le Sc. med. Torino*, 1880, iv. 221-246.

<sup>3</sup> *Ewald* and *Kühne*, "Die Verdauung als histologische methode. Ueber einen neuen Bestandtheil des Nervensystems," *Verhandl. des Naturhist med. Vereins zu Heidelberg*, Bd. i., 1876.

<sup>4</sup> *Rumpf*, "Zur Hist. der Nervenfasern und des Axencylinders," *Sonder abdr. aus den Untersuchungen des Physiol. Instit. der Universität. Heidelberg*, Bd. ii. heft 2, 1878.

<sup>5</sup> *Tizzoni*, "Sulla patologia del tessuto nervoso-osservazione ed esperimenti sulla istologia normale e patologica della fibra nervosa," *Archiv per le Sc. med.*, vol. iii. fasc. 1, 1878.

<sup>6</sup> *Koch*, "Zur Kenntniss der Markhaltigen Nervenfasern," *Tageb. der 51 Vers. deutschen Naturf. und Aerzte in Kassel*, 1878, s. 262.

<sup>7</sup> *Fleming*, "Observations on the Histology of Medullated Nerve-fibres in Man and Rabbits," *Jour. Anat. and Phys.*, 1897, vol. xxxi. p. 397.

is also evidence of an additional network of fibres or strands running between the axis-cylinder and the periphery.

*M'Carthy* has shown that after a nerve has been hardened with picric acid or ammonium chromate, the medullary sheath contains minute rod-like structures, which pass radially between the axis-cylinder and the primitive sheath so as to give the cross-section of a fibre the appearance of a wheel. The rods stain with carmine and hæmatoxylin, which do not stain the myelin. It is not possible to isolate the rods as separate elements, for they are not distinct from one another, but united.

*Geddoelst* regards the neuro-keratin network as the reticulum of the original protoplasmic cell from which the medullary sheath has been formed.

*Chittenden*, *Leydig*, *Palulino*, *Joseph*, and *Schiefferdecker* all hold that there is a pre-existent neuro-keratin supporting network; whereas, on the other hand, a large number of observers—*Engelmann*, *Gerlach*, *Waldstein* and *Weber*, *Hesse*, *Pertik*, *Kölliker*, *Boveri*, *Lawdowsky*, *Von Büngner* and *Stroebe*—consider that either the network is due to post-mortem change or is an artificial product of the reagents used.

*Ranvier*, *Garl*, and *Heymans* believe that the medullary sheath contains an albuminous substance, which is artificially separated and deposited as a network by the reagent employed.

*Lantermann*, *Von Stilling*, *Rowlanowski*, and *M'Carthy* all believe that there is a system of hollow canals in the sheath which are connected with the axis-cylinder. They think that the network-like appearance is due to this.

There can be no doubt that the medullary sheath contains the material known as neuro-keratin, but there are several facts which seem to oppose its existence as a network in the living nerve fibre. Its very variable appearance; the difference in the size of the meshes even in the same fibre; the fact that, as *Gerlach* has shown, the character of the network varies with the strength of the alcohol used, seem to point to the view that it is due to the artificial precipitation by the alcohol or other reagent used of some material containing so-called neuro-keratin, which enters into the constitution of the medullary sheath.

#### METHOD.

Most of the sections have been obtained from the sciatic nerves of dogs and cats, but other nerves were also employed, as well as posterior root-ganglia and spinal cord. Occasionally human nerve was used. The nerves were carefully removed immediately after death, care being taken to avoid injury by undue manipulation; they were then suspended in 5 per cent. formalin (*i.e.*, 2 per cent. formaldehyde) until hardened. Formalin was invariably the hardening reagent used, since it rapidly

kills the tissue and hardens without causing any obvious swelling or shrinkage. Formalin-hardened tissue also readily lends itself to the special method of staining employed.

Sections were cut with the freezing microtome, the piece of nerve being simply dried with blotting-paper, then surrounded with gum, and frozen, without previously soaking it in gum. The sections were preserved in 5 per cent. formalin until required.

The further treatment consisted in staining the sections by one or other of the modifications of the Weigert-Pal method introduced by Bolton.<sup>1</sup> The sections were mordanted by placing them for twenty-four hours in the cold, in a 2 per cent. solution of ammonium molybdate, iron alum, or uranium acetate. This process was sometimes hastened by placing the sections in the solution in an incubator at 40° C. After well washing with distilled water, the sections were stained for some hours in the cold in acid hæmatoxylin, or for about two hours in an incubator at 40° C., and then after again well washing with water, they were differentiated by Pal's method. The sections were first placed for a few seconds in a solution of potassium permanganate, then transferred to Pal's solution, after which the bleaching baths were alternated until the required differentiation was obtained. The sections were then washed in distilled water, dried with blotting-paper on a section-lifter, and transferred to absolute alcohol for a few seconds (if the alcohol be made very slightly alkaline, sections can remain in it longer without harm), then again dried and placed in chloroform, then without drying passed into xylol and mounted in xylol balsam. Latterly I have also used a new method of differentiation, chiefly for sections mordanted in ammonium molybdate, discovered by Bolton. This method is far simpler and quicker than Pal's method, and equally good results are obtained. The sections are simply placed in a moderately dilute solution of ammonia, when the unattached lake is quickly dissolved out, leaving differentiation complete.

Some sections were cut in paraffin, fixed on the slides by Gaule's method, and then mordanted, stained, and differentiated

<sup>1</sup> Bolton, "On the Nature of the Weigert-Pal method," *Journ. Anat. and Phys.*, vol. xxxii. p. 247.

as above. The results were identical with those obtained by the other methods.

The Weigert-Pal method was, until recently, regarded as a specific method for staining the medullary sheath of nerve fibres. But Bolton,<sup>1</sup> in a recent investigation on "The Nature of the Weigert-Pal Method," has shown that it is "a method of dyeing fibrils which comprises three distinct operations: the mordanting of the fibrils, the formation of a lake in them, and finally the removal of the stain by oxidation from nearly every other part of the complex tissue under treatment." He further showed that the tissues which are most readily mordanted, and therefore in which the hæmatoxylin lake is most intensely deposited, are those possessing the greatest actual or potential metabolism. Thus this method can be applied to tissues other than nervous, which contain fibres of high metabolic activity, surrounded by ground substances of low metabolism. Thus when sections of kidney are submitted to the process, a beautiful staining of the kidney tubules results, though naturally, owing to the coarseness of the fibres (tubules), the section is only of value under a low power. Involuntary muscle-fibres can similarly be stained in a section, for instance, of intestine. Sections of parenchymatous structure, such as the liver, where metabolism is approximately equal throughout, remain diffusely stained, or are entirely decolorised according to the extent to which the bleaching process is carried out.

The reason, therefore, that the method is only of practical value in the nervous system, is not that it is a specific staining for myelin, but because here alone are minute fibres of considerable length and of at any rate high potential metabolism. As further evidence of its action may be mentioned, the non-staining of fibrous and elastic tissues and of neuroglia, in all of which the metabolic activity is low, while blood-corpuscles readily stain and are difficult to decolorise, and the nucleoli of nerve-cells often remain black, even after over-differentiation and decolorisation of many nerve-fibrils.

This method is therefore particularly applicable to the study of the medullary sheath, where we have presumably to deal with two structures differing greatly in metabolic activity—the

<sup>1</sup> *Jour. Anat. and Phys.*, xxxii. p. 247.

myelin and the supporting network or stroma. With careful differentiation it should then be possible to obtain the part with the higher metabolism deeply stained, the other with the lower metabolism decolorised. This, as I shall show, is actually the case.

### HISTOLOGY.

In a typical longitudinal section of a nerve prepared as above, and examined under a low power of the microscope, each nerve fibre is seen to be stained in a peculiar manner. The axis-cylinder is more or less deeply stained in its whole length, but the medullary sheath is only partially stained, deeply stained portions alternating regularly with unstained portions, thus giving to the nerve fibre a characteristic beaded or varicose appearance. The stained parts are funnel or cone-shaped with their apices in any short length of a fibre pointing in the same direction (fig. 1). Bolton,<sup>1</sup> in a paper on "The Range of Applicability of Certain Modifications of the Weigert-Pal Process,"

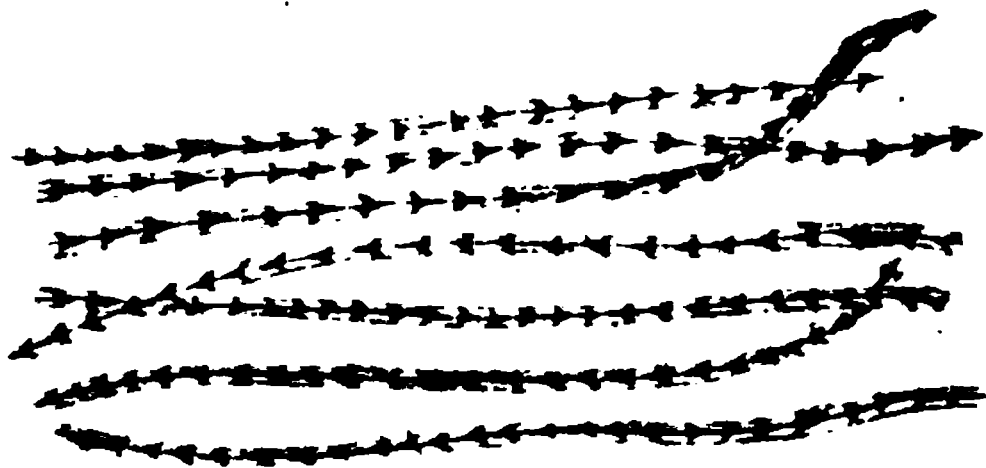


FIG. 1.—Longitudinal section of sciatic nerve of cat. Slightly teased. Showing cones only. Low power.

published two micro-photographs, one of a longitudinal section of a posterior root-ganglion of a cat, the other of a transverse section of a dog's sciatic nerve, in which these appearances are seen and briefly referred to.

On carefully examining a single fibre with a higher power the stained portions of the sheath are observed to be actual cones or funnels, each possessing a definite structure, which is constant in all the cones of the same fibre.

<sup>1</sup> *Jour. Anat. and Phys.*, vol. xxxiii. p. 294-5, Pl. VII.

If the section has been strongly mordanted and under-differentiated, the cones appear to be solid and structureless, and the axis-cylinder is deeply stained. The base of the cone has the same diameter as the fibre itself, so that it occupies the whole circumference of the fibre lying immediately beneath the primitive sheath. The apex of each cone is pierced by the axis-cylinder, which therefore occupies the axes of all the cones (fig. 2).

If the section has been moderately mordanted and carefully differentiated the cones are not complete, but are composed of

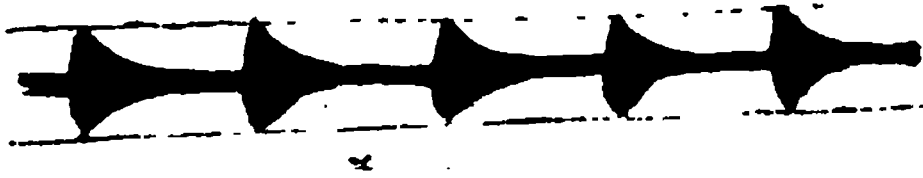


FIG. 2.—Single fibre of above section more highly magnified. Segments of cones are undifferentiated. Peripheral protoplasmic sheath is faintly stained near bases of cones.

several separate pieces, which are deeply stained, separated by gaps where the stain has been washed out (fig. 3). These segments are placed at regular distances apart, each passing from the primitive sheath to the axis-cylinder. All the segments of the

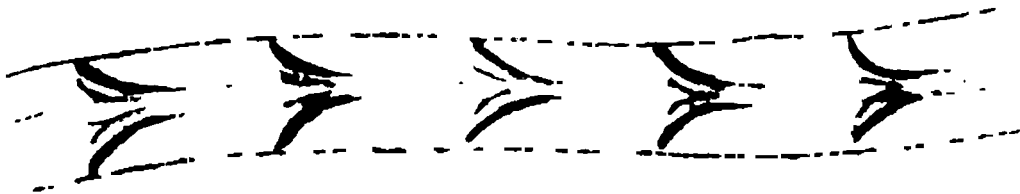


FIG. 3.—Portion of fibre from cat's sciatic nerve. Shows cones differentiated to show segments.

cone are not in focus at one time, but they can be made out by carefully focussing up and down; they are six in number, but this is better seen in transverse sections. Each segment is slightly curved, the concavity being outwards, so that on the whole the surface of a cone is nearer to the axis-cylinder than to the primitive sheath. At the apex of a cone the segments often appear to be united, and continued around the axis-cylinder for a short distance as a sheath. The axis-cylinder in moderately mordanted sections loses its stain before the



segments of the cones, and so in many fibres the axis-cylinder is unstained except near the cones.

The cones are placed at regular distances apart along a fibre. They do not overlap or fit into one another. There is usually a short distance between the base of one cone and the apex of the next, which distance may be as long as the length of a cone.

The cones all lie in one direction in the same internode, but so far as can be made out, they change their direction at each node.

In most sections besides the cones there can be seen a faintly-stained substance lying just beneath the primitive sheath. In moderately mordanted fibres the substance is only seen near the bases of the cones, where it is stained fairly deeply, but as it passes into the interval between two cones the stain gradually disappears and the substance becomes invisible.

When the middle of the fibre is in focus, only that portion of the substance lying immediately beneath the primitive sheath where it is cut by the plane of the focus can be seen; this gives to it the appearance of two fine points projecting like barbs from the base of the cone (Plate L. fig. 1).

In over-mordanted or under-differentiated fibres the whole of this substance is deeply stained so as to obscure the cones, and then it is seen to form a continuous sheath lying immediately beneath the primitive sheath. In other fibres, again, the whole of the sheath is stained, but it has shrunk from its place beneath the primitive sheath towards the axis-cylinder, *i.e.* it has undergone plasmolysis; but this only occurs in the spaces between the cones; where the bases of the cones reach the primitive sheath the substance is held in position and prevented from shrinking. In many places the more deeply stained cones can be seen through the less deeply stained sheath. These features can be made out in Plate L. fig. 2, taken from a longitudinal section of a cat's spinal ganglion, if it be examined in a good light with a lens. This sheath is still better seen in transverse sections. Very often the place of this sheath is occupied by a network resembling somewhat the neuro-keratin network of Kühne; this will be described in detail later.

Perhaps the appearances seen in transverse sections of a nerve are even more interesting. In some sections the axis-



cylinder is the most deeply stained part of the fibre; it is seen lying in the middle of a ring of faintly-stained or unstained medullary substance. In other sections the medullary sheath is the more deeply stained part, the stain having nearly been washed out from the axis-cylinder, which is therefore almost colourless; this is usually the case with large fibres that have been over-mordanted. But when the fibres have been moderately mordanted and carefully differentiated, the majority of the fibres show the medullary sheath with its constituent parts distinguished. It thus appears to be only partially stained, the ring of medullary substance being broken up by gaps into six segments (Plate LI. fig. 3). This segmented ring does not occupy the whole of the space between the axis-cylinder and the primitive sheath, but varies in position; thus, it may lie immediately beneath the primitive sheath, the space between it and the axis-cylinder being unstained; or it may immediately surround the axis-cylinder, having an unstained portion outside it, and between it and the primitive sheath; or it may occupy some position between these two extremes, the medullary substance both within and without the ring being unstained.

In other fibres there is a thin ring immediately beneath the primitive sheath, and another surrounding the axis-cylinder, both of which are complete and unsegmented; the latter is only distinctly seen when the axis-cylinder is unstained. In many fibres their presence is obscured by the larger segmented ring, but when this is near the axis-cylinder the thin unbroken ring beneath the primitive sheath can be seen, and *vice versa*. They can both be seen when the segmented ring occupies an intermediate position. Generally these rings, although unbroken, show six slight enlargements at regular intervals, evidently corresponding to the six segments of the larger ring. In some fibres in which the medullary ring broken up into segments lies beneath the primitive sheath, it can be seen by careful examination that the six segments are united and the ring so completed by a thin line beneath the primitive sheath. All these various points can be easily made out by examining the micro-photograph (Plate LI. fig. 3) with a lens.

The usual number of segments in a ring is six, but occasion-

ally a greater or less number may be seen ; for instance, five, seven, or eight. Five is the least number I have observed, and then it is nearly always evident that one of the segments has dropped out during manipulation, for a space much larger than usual is seen between two of the segments, the remaining spaces being of the regular size. Fibres showing more than six segments are comparatively rare, and in some of these the extra segment or segments are in a different plane to the others, and so may not belong to the same structure ; a possible explanation of this will be given later in discussing the network mentioned above ; in some sections with more than six segments one or more of them are smaller than the rest, and so possibly have been formed by the breaking-up of an ordinary segment. But probably in a few fibres the number of segments may be normally greater than in others, and such fibres seem to be those of greater size.

In many fibres, especially in sections of moderate thickness, the segments can be traced by focussing up and down from the primitive sheath to the axis-cylinder, to which they converge. Thus on looking at a section of a fibre focussed for the peripheral part of the segments, a broken ring is seen beneath the primitive sheath, and from each segment of the ring a line getting gradually more indistinct can be traced to the axis-cylinder to the ring surrounding which all the lines converge.

These appearances seen in cross-section are easily explained by reference to the longitudinal sections. In longitudinal section each fibre was seen to contain a chain of hollow cones, each cone being made up of several segments. In transverse sections we have these cones cut across in different places. The segments of the rings are the transverse sections of the segments of the cones, and the varying positions of the ring in relation to the primitive sheath and axis-cylinder are seen to be due to the different places in which the cones have been cut across. When a cone is cut across at its base, the ring lies immediately beneath the primitive sheath ; if the cone is cut across near its apex, then the ring surrounds the axis-cylinder ; and, lastly, if the cone is cut midway between base and apex, then the ring seen in transverse section lies midway between the axis-cylinder and the primitive sheath, the medullary sub-

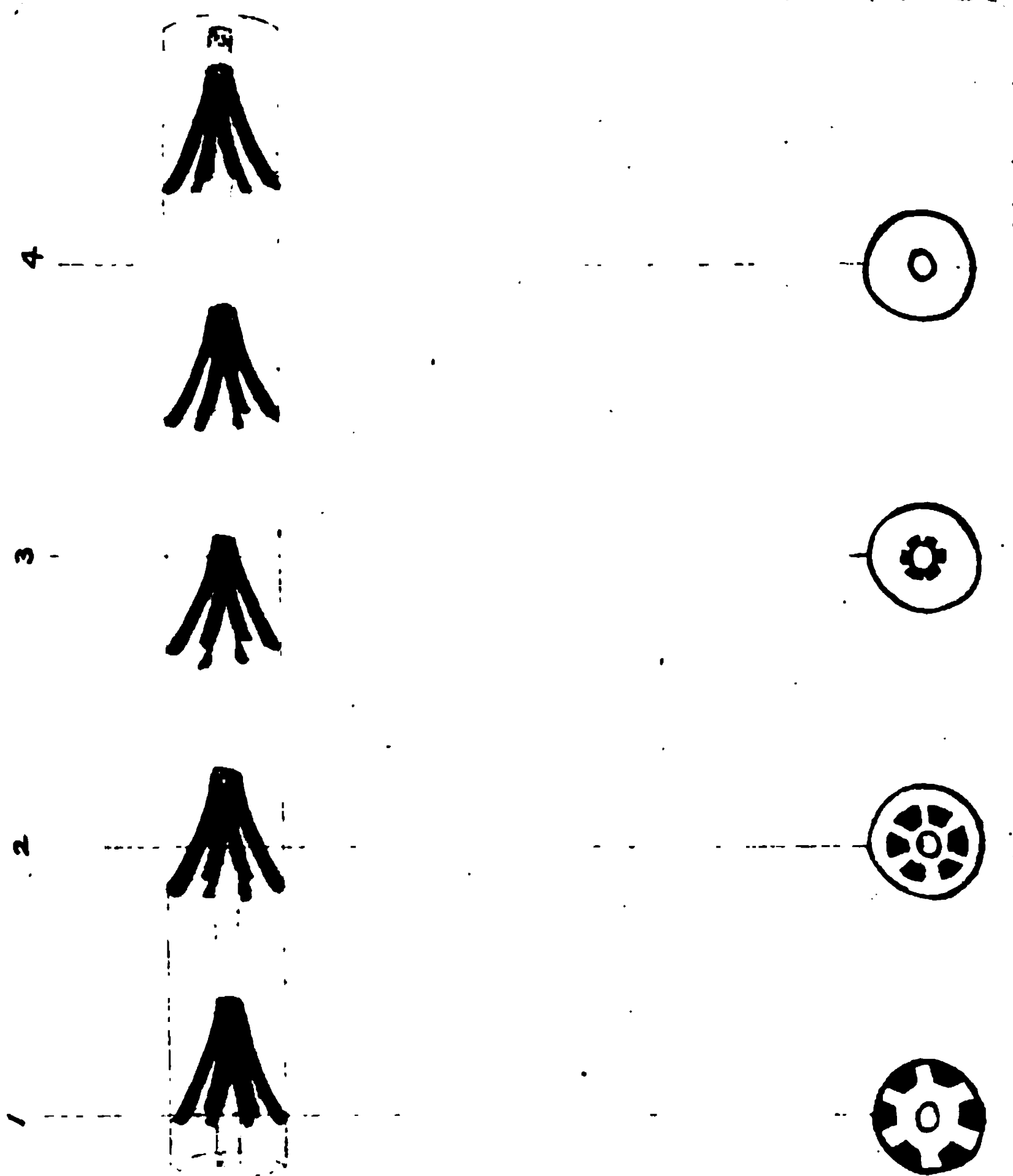


FIG. 4.—Diagram of relation between longitudinal and transverse sections, showing cones cut across at different levels: 1, at base of cone; 2, through middle of cone; 3, through apex of cone; 4, through interval between two cones. In 1, 2, and 3 the cone segments and protoplasmic sheaths are seen. In 4 only the thin protoplasmic sheaths beneath primitive sheath and around axis-cylinder are visible.

stance lying inside and outside the ring being unstained except, perhaps, a faint ring beneath the primitive sheath or around the axis-cylinder. Again, if the section happen to pass through the interval between two cones, the segmented ring is absent, and only the thin unsegmented rings beneath the primitive sheath and around the axis-cylinder are to be seen. These rings correspond to the continuous sheaths of stainable substance existing in these situations, and described in longitudinal section above.

The cones and other stained portions must chemically be regarded for the following reasons to be highly protoplasmic.

1. They are readily mordanted and stained, the stain being with difficulty removed, often remaining in the medullary sheath when completely washed out from the axis-cylinder. This, as has been shown, is characteristic of substances of high metabolism, such as a highly protoplasmic structure would be.

2. Nerve contains a large amount of proteids (30–35 per cent. of the whole solids), and since the axis-cylinder occupies but a small portion of the total bulk of a fibre, a large proportion of these proteids must be contained in the medullary sheath, and presumably as protoplasm.

3. The cones cannot be composed of neuro-keratin, since this substance would not be stained by this method—neuroglia, for instance, remaining unstained. The quantity of neuro-keratin in nerve is also very small (0·3–0·6 per cent.), whereas the cones occupy a fair amount of the total bulk of the medullary substance.

Differentiation must, of course, take place very differently in the two kinds of sections. In longitudinal sections the differentiating fluids have to penetrate the primitive and medullary sheaths before reaching the axis-cylinder, which is therefore usually well stained in longitudinal sections; the peripheral part of the medullary sheath will be more liable to have its stain washed out than the central part near the axis-cylinder, hence the protoplasmic layer beneath the primitive sheath is usually unstained; the cones are well stained, and the protoplasmic layer around the axis-cylinder is also usually well stained, and is then indistinguishable from the axis-cylinder.

The segments of the cones seem to hold their stain longer than any other part of the fibre, and are therefore presumably the most highly protoplasmic.

In cross-sections the differentiating fluids are able to gain easier access through the cut surfaces to all parts of a fibre; and since the axis-cylinder is composed of tubular fibrils, the fluids probably penetrate more easily into its midst than into the medullary sheath, hence the fact that the axis-cylinder is often unstained in transverse sections. The peripheral protoplasmic layer is not now more exposed to the fluids than the other parts of the sheath, as it was in longitudinal sections, it is therefore more readily seen.

The structure of the medullary sheath, as revealed by these sections, seems to be as follows:—

The protoplasmic framework, which contains the myelin, consists of, firstly, two thin layers, one beneath the primitive sheath, the other around the axis-cylinder; these sheaths or layers seem to be continuous at the nodes, *i.e.* the peripheral sheath is reflected there on to the axis-cylinder to form the central sheath; secondly, of a chain of cones connected with both layers of protoplasm, the base of a cone being in the peripheral layer, the apex in the central layer, each cone being made up of six segments placed at regular distances apart, and converging from the primitive sheath to the axis-cylinder.

The myelin is thus contained in conico-cylindrical segments, which, however, are not entirely separated from one another by septæ, but communicate through the spaces between the segments of the cones. These segments do not correspond to the medullary segments described by Schmidt and Lantermann. The incisures of Schmidt do not occur in the situations of the cones, but in the highly fatty myelin between them, which is the least resistant part of the medullary substance, and consequently the part most likely to give way, either when the fibre is stretched or the medullary substance shrinks from the action of reagents. This would account for their great variability in number, size, and direction, since rupture would not necessarily take place in every space between the cones, or in the same oblique direction, but just where the resistance happened to be least.

The cones can be made out in transverse sections of spinal cord, though with more difficulty, possibly the absence of a primitive sheath altering the manner of differentiation. Also less supporting framework would be needed in the central nervous system, where each fibre is closely invested by neuroglia.

In most sections, instead of having only the cones stained, the fibres show a network which is probably identical with that described by Kühne as the neuro-keratin network, but which, for reasons mentioned above, is more probably protoplasmic.

The network does not stain regularly along the whole length of a fibre, but appears irregularly broken up into shorter or longer pieces, which alternate with places where the network is invisible, and in which one or more cones may be seen.

The network produced by this method is often very much more regular than the so-called neuro-keratin network is described to be. In most fibres there are enlargements at the nodes of the network. Thus, often there are circles of dots beneath the primitive sheath, the circles occurring with fair regularity; the dots are connected with the others in the same circle, so completing it, and they are also connected by longitudinal lines with the corresponding dots in the next circles. The appearance given is that of a network with long rectangular meshes having enlargements at each node. The number of enlargements in a circle is often the same as the number of segments in a cone—six (Plate LI., fig. 4).

But generally the meshes are more irregular than this, though still having enlargements at the nodes. In other fibres the enlargements are absent, the strands of the network being everywhere of the same thickness.

In the larger fibres the network is more likely to be broken up into small portions, and to have regular meshes; while in the smaller fibres considerable lengths of the network are often stained, the meshes being very irregular.

The nodes of the network may in transverse sections be mistaken for the segments of the cones, and so may be responsible for the extra number of segments when these appear to exceed six.

This network I believe to be an artificial production. It cor-

responds in position to the peripheral protoplasmic sheath, and is evidently produced from that by the action of reagents or by mechanical injury. This layer of protoplasm is in a position where it is very liable to injury. The breaks in the continuity of the network correspond in position and other features with the incisures of Schmidt, which seems to show that the ruptures which occur there involve the peripheral protoplasmic sheath also. A very probable explanation of the formation of this network, I think, is that it is not a precipitation of neuro-keratin by the action of alcohol or other reagents, but the result of the physical forces of tension and cohesion in this layer of semi-fluid protoplasm. It is not difficult to see how on this theory such a network would be produced. Starting with a thin homogeneous layer of semi-fluid substance, such as protoplasm, more or less adherent by one surface to a membrane, the primitive sheath, it is clear that if tension was produced in this layer either by its own shrinkage or by the stretching of the fibre as a whole, a point would be reached at which its power of cohesion would be insufficient to keep the layer intact, and it would give way in places while still cohering in others, thus forming a fenestrated layer or network, similar to the cohesion figures produced, by pouring a drop of oil on to the surface of water. If the shrinkage still continued the protoplasm would tend to collect in small masses or globules, the connection between which, *i.e.* the strands of the network, would become slighter and slighter. Hence the particular form the network would take in any particular section would depend to a large extent upon the regularity and rapidity with which the hardening process was effected. If the fibre is rapidly fixed and prevented from further shrinking, the network should have coarse strands and hardly any enlargement of the nodes; whereas if hardening has taken place slowly, the nodes should be markedly enlarged and the strands fine. This is what actually occurs. It is also found that the network is most easily produced by those reagents, such as absolute alcohol, formalin, etc., which, by attracting water from the protoplasm, would cause its shrinkage; and in sections, *e.g.* from a spinal ganglion hardened in this way, it is found that those portions of the fibres which are near the periphery, and therefore more intimately in

contact with the hardening fluid, contain networks, while those in the interior often have their peripheral protoplasmic sheaths intact.

The network I believe from the manner of its staining to be protoplasmic, and not to be composed of neuro-keratin, as is usually held. The only evidence in favour of the latter view is the great resistance the network shows to digestive fluids, but nuclein also possesses this character, and would, in fact, be indistinguishable micro-chemically from neuro-keratin. It is far more reasonable, then, and more in accordance with modern ideas of the chemistry of the cell, to hold the view that the network is protoplasmic, and therefore must contain a large amount of nucleo-proteids; during digestion the proteid portion would be destroyed, leaving an insoluble residue of nuclein.

#### CONCLUSIONS.

1. The medullary sheath examined by the Weigert-Pal method consists apparently of two parts—myelin and a supporting framework.

2. The latter, as seen in sections prepared by the Weigert-Pal method, probably consists of two thin protoplasmic sheaths, one beneath the primitive sheath, the other surrounding the axis-cylinder; and of a chain of hollow cones with their bases in the peripheral protoplasmic sheath and their apices in the central sheath.

3. Each cone is composed of six segments, placed at regular distances apart, and converging from the primitive sheath to the axis-cylinder.

4. These cones are apparently protoplasmic in nature.

5. The neuro-keratin network, as usually described, is probably artificially produced from the protoplasmic layer beneath the primitive sheath. This network may not be composed of neuro-keratin but of protoplasm; its resistance to digestive fluids being due to the contained nuclein.

6. The incisures of Schmidt or Lantermann's slits may be ruptures in the medullary substance between the cones.



FIG. 1.

FIG. 2.

DR WINN.



FIG. 3

FIG. 4.



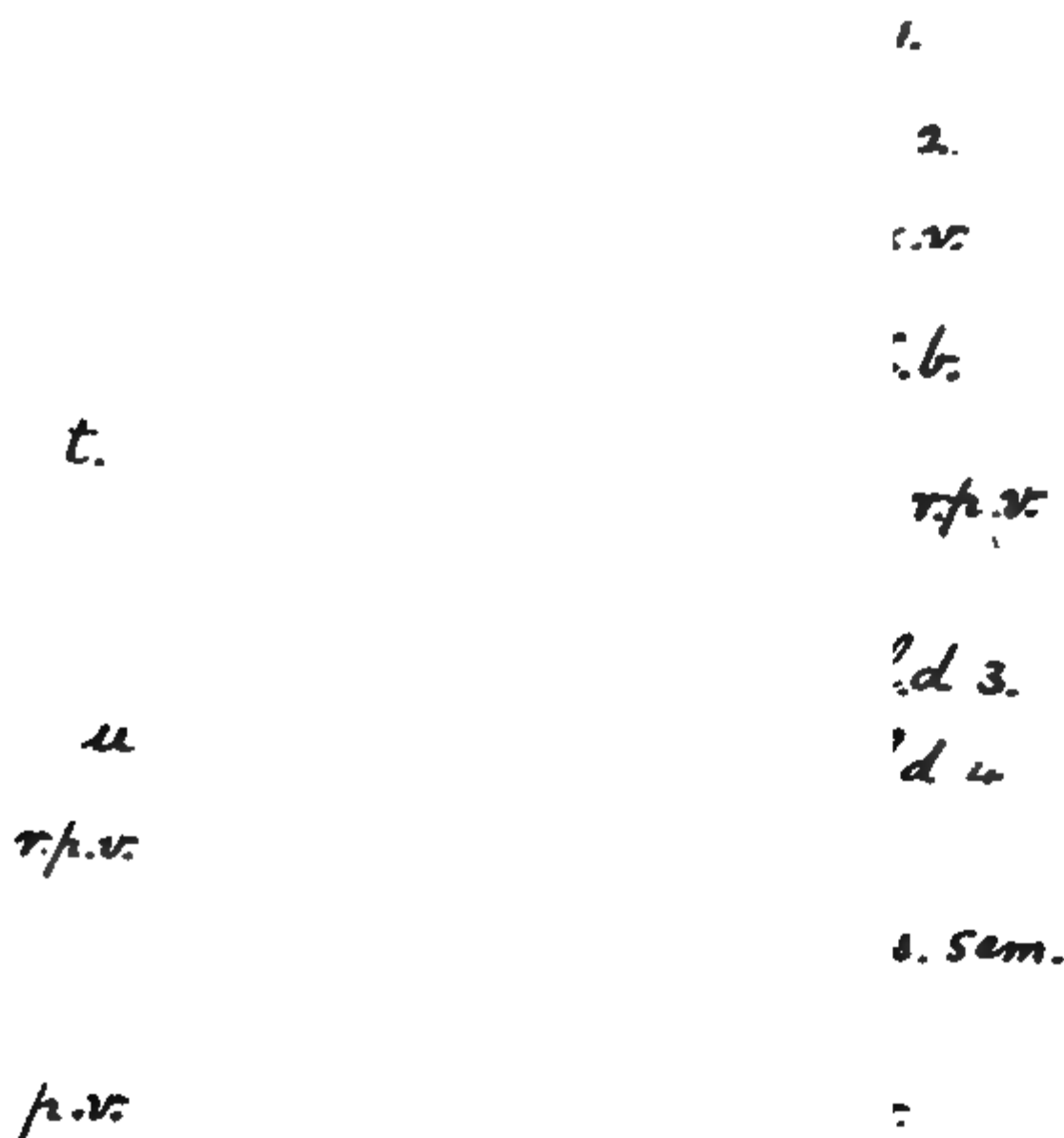
The above conclusions agree in substance with the description given by Bolton in the paper previously referred to, and are to be considered as the preliminary results of a more extended investigation in which I am at present engaged.

In conclusion, I have gratefully to acknowledge the very valuable advice and criticism received from Dr J. S. Bolton. I am also indebted to him for the preparation of the excellent micro-photographs which accompany this paper.

UNUSUAL ARRANGEMENT OF THE RENAL PORTAL  
VEIN IN THE FROG (*Rana temporaria*). By THOMAS  
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THE specimen which forms the subject of this note occurred last year in the ordinary course of practical work in my laboratory, and my attention was called to it by one of my pupils. The specimen appears to throw some doubt on the currently accepted view of the development of the renal portal veins, and for this reason I now describe it. The drawing given below will afford a fair idea of the arrangement which was present. The animal was a well-developed male specimen of *Rana temporaria*. On the right side the renal portal vein was normal in position and extent, and the renal and spermatic veins opening into the post-caval were arranged in the usual way. On the left side, however, instead of the renal portal vein terminating in the normal way along the outer border of the kidney, it was continued forwards in close apposition to the kidney, curving round its anterior end as a large vessel to open directly into the post-caval vein at a level with the anterior end of the testis. On the right side the renal portal received only one dorso-lumbar vein, but on the left, it and its abnormal continuation into the post-caval received altogether four lumbar veins. The most anterior of these was slender, and was traced to the foramen between the fifth and sixth vertebræ, and terminated in the abnormal vein near the most anterior part of the kidney. The next was considerably larger, was traced forwards to the foramen between the sixth and seventh vertebræ, and similarly ended in the abnormal prolongation of the renal portal. The other two lumbar veins occupied the positions in which the dorso-lumbar veins are usually found. Just before its junction with the post-caval, the abnormal vein received the left anterior renal and spermatic vein, with prominent tributaries from the fatty body; and its entrance into the post-caval was at the level of the anterior renal and spermatic vein of the right side. There was no marked

difference in the size of any of the organs of the left side as compared with the right, and although of necessity a considerable part of the blood conveyed by the left renal portal would flow on into the post-caval without traversing the capillaries of



*k.* kidney; *t.* testis; *f.b.* fatty body; *u.* ureter; *ves. sem.* vesicula seminalis; *p.c.v.* post-caval vein; *r.p.v.* renal portal vein; *s.v.* sciatic vein; *f.v.* femoral vein; *p.v.* pelvic vein; *c.v.* abnormal vein connecting the left renal portal with the post-caval. *l.d. 1*, first left lumbar vein; *l.d. 2*, second left lumbar vein; *l.d. 3*, *l.d. 4*, third and fourth left lumbar veins.

the kidney, this organ presented no apparent abnormality, and the left renal veins were not obviously smaller than the right.

The chief interest attached to this specimen lies in the interpretation which is to be assigned to it, in view of the develop-

ment of the post-caval and renal portal systems. Most of our knowledge of the development of these vessels, both in Amphibia and Fishes and in Man and Mammals, is due to Hochstetter.<sup>1</sup> During the early stages of tadpole-life, the main veins of the posterior part of the body are the paired posterior cardinals. These are formed in special relation to the pronephros, which in the frog is a well-developed functional organ during early tadpole-life. At this stage the anterior parts of the posterior cardinal veins are very large and dilated, and almost surround, as a vascular network the pronephros with its three nephrostomes and glomerulus. The posterior parts, however, are more slender, and receive a few somatic veins from the hinder part of the body wall. Later on they receive the iliacs, and, it is said, approximate to one another and unite. The posterior cardinals are certainly very prominent vessels, and are perhaps best seen in sections, a little posterior to the heart in tadpoles, from 10 to 14 mm. in length, and continue to be well developed as long as the pronephros remains functional. Shortly after the establishment of the posterior cardinals, the post-caval vein begins to form, and in its origin is quite independent of the cardinals. In a tadpole, 10 to 12 mm. in length, the post-caval is a distinct vessel, which can be traced backward near the middle line, from the sinus venosus in close apposition to the left dorsal surface of the liver, from which it receives the hepatic veins, towards the rudiments of the mesonephros, from which it shortly receives some small renal veins. At this level it is said to become continuous with the two posterior cardinals, which are believed to unite together to form the lower part of the adult post-caval. For a time, apparently, the blood from the lower parts of the body can return by either the cardinals or the post-caval, but gradually the current seems to become more and more diverted into the post-caval, by the gradual dwindling of the anterior parts of the cardinals, as the pronephros becomes more and more degenerate, until during metamorphosis the anterior parts of the posterior cardinals disappear entirely. The foregoing is a summary of

<sup>1</sup> Hochstetter, F.—“Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische.”—*Morphol. Jahrbuch*. xiii., 1888.



what is currently taught of the post-caval and posterior cardinals in Amphibia.

There is no doubt, according to Hochstetter,<sup>1</sup> that the post-caval vein in Man and Mammals is formed in two sections—an anterior part as far back as the renal veins developed independently, and a posterior section formed from the right posterior cardinal vein. The left posterior cardinal, on the other hand, ultimately disappears from the level of the renal veins backward. Apparently, then, there is some difference between the ultimate fate of the hinder parts of the posterior cardinals in Amphibia as compared with Mammals. This difference may not, of course, in reality exist, and I rather suspect that no part of the post-caval in the frog is formed from the posterior cardinals.

The most probable explanation, I think, of the abnormal vein in the specimen in question is that it is a persistent part of the left posterior cardinal vein, which normally disappears during the later parts of larval life. If this interpretation be correct, it would follow that the greater part, if not the whole, of the left renal portal vein is formed from the lower end of the left posterior cardinal; and if this is the case, it seems to me most probable that the right renal portal vein is similarly formed from the right posterior cardinal, and that unlike the arrangement in Mammals no part of the post-caval is developed out of either of the cardinals.

On the other hand, it is generally taught that the renal portals are developed at a later stage than the post-caval and quite independently of the posterior cardinals by an antero-posterior anastomosis of some of the lumbar or vertebral veins. In the light of the specimen under consideration, I feel that this, the currently accepted view of the development of the renal portals, is improbable, and that these veins are in reality the persistent hinder parts of the posterior cardinals. In favour of

<sup>1</sup> Hochstetter—"Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten," *Morphol. Jahrbuch.* xiii., 1888. See also, by the same author: "Ueber die Bildung der hinteren Hohlvene bei den Säugethieren," *Anat. Anzeiger*, 1887, p. 517; also "Ueber den Einfluss der Entwicklung der bleibenden Nieren auf die Lage des Urnierenabschnittes der hinteren cardinalvenen," *Anat. Anzeiger*, 1888; also "Ueber das Gekröse der hinteren Hohlvene," *Anat. Anzeiger*, 1888.

this view, the following facts and arguments should be borne in mind :—

1. In the frog, as in Man and Mammals, the iliac and somatic lumbar veins at an early stage directly join the posterior cardinals.

2. In Man and Mammals, the iliacs and somatic lumbar veins eventually become connected with the post-caval, by the conversion of that part of the right posterior cardinal *which lies behind the renal veins* into the posterior section of the post-caval.

3. In the frog, the post-caval vein *does not extend backwards* beyond the renals, and the iliacs and lumbar veins do not in the adult, or indeed at any period, open into it.

4. In the frog, the iliacs in the adult are continuous with the renal portals, which receive also the somatic lumbar veins as the posterior cardinals do in the embryo.

Bearing in mind these facts, I am distinctly of opinion that the currently accepted view of the development of the renal portals is improbable, for it seems to me extraordinary that new antero-posterior anastomosis of the somatic lumbar veins should be formed and should then acquire a connection with the iliacs, when these vessels already have longitudinal communication through the posterior cardinals into which they open. I am doubtful also of the statement that in the frog the posterior parts of the posterior cardinals persist as the hinder section of the post-caval. On the other hand, the statement that the post-caval becomes connected in embryonic life with the posterior cardinals in the neighbourhood of the developing mesonephros, as it does in Mammals, is probably correct. In fact my specimen seems to indicate that this is so, and that the abnormal vein in question is the persistent connection of the left posterior cardinal with the post-caval, the corresponding connection of the right side having disappeared in the normal way.

To settle the point, I have begun an examination of sections of frog tadpoles, but have not yet studied a sufficient number of stages to decide exactly how the renal portals are developed. These additional stages, I hope to obtain shortly.

## NOTES ON THE DISSECTION OF TWO CLUB FEET.

By R. TAIT M'KENZIE, B.A., M.D., *Demonstrator of Anatomy, McGill University, Montreal.*

THE two specimens described in this paper were taken from a young adult male subject, suffering from double congenital talipes equino-varus.

The deformity was almost exactly similar in both feet, so that it was decided to leave intact the tendons, ligaments, and muscles in one, while the other was completely dissected, in order that the bony changes could be more completely studied and clearly seen. Both feet were in extension, with inversion and marked rotation inward. The dorsal surface was convex, and the weight of the body was supported principally by the base of the fifth metatarsal and the external tubercle of the os calcis.

On removing the skin and superficial fascia, the anterior annular ligament was found strongly developed; the external annular ligament was scarcely to be seen, while the internal annular ligament presented an upper border, sharply concave, and a lower border giving extensive attachment to the abductor hallucis, as seen in figure 1, B. The plantar fascia was contracted and crossed by transverse bands, and the muscles of the first layer were widely separated. The flexor brevis digitorum was atrophied, and had three tendons only.

In the second layer the accessorius had only one origin, the external, and its fibres ran almost directly across the foot in the effort to retain the displaced tendon of the flexor longus digitorum.

All the muscles of the leg were atrophied. The tendo Achillis on section was not larger than a split lead pencil, and was attached to the upper and outer border of the posterior surface of the os calcis, the direction of its pull being such as to constantly increase the internal rotation of the bone about its centre.

The tendon of the tibialis posticus deeply grooved the tibia in the normal position, and spread out into a flat fibro-cartilaginous plate like an inter-articular fibro-cartilage, between the

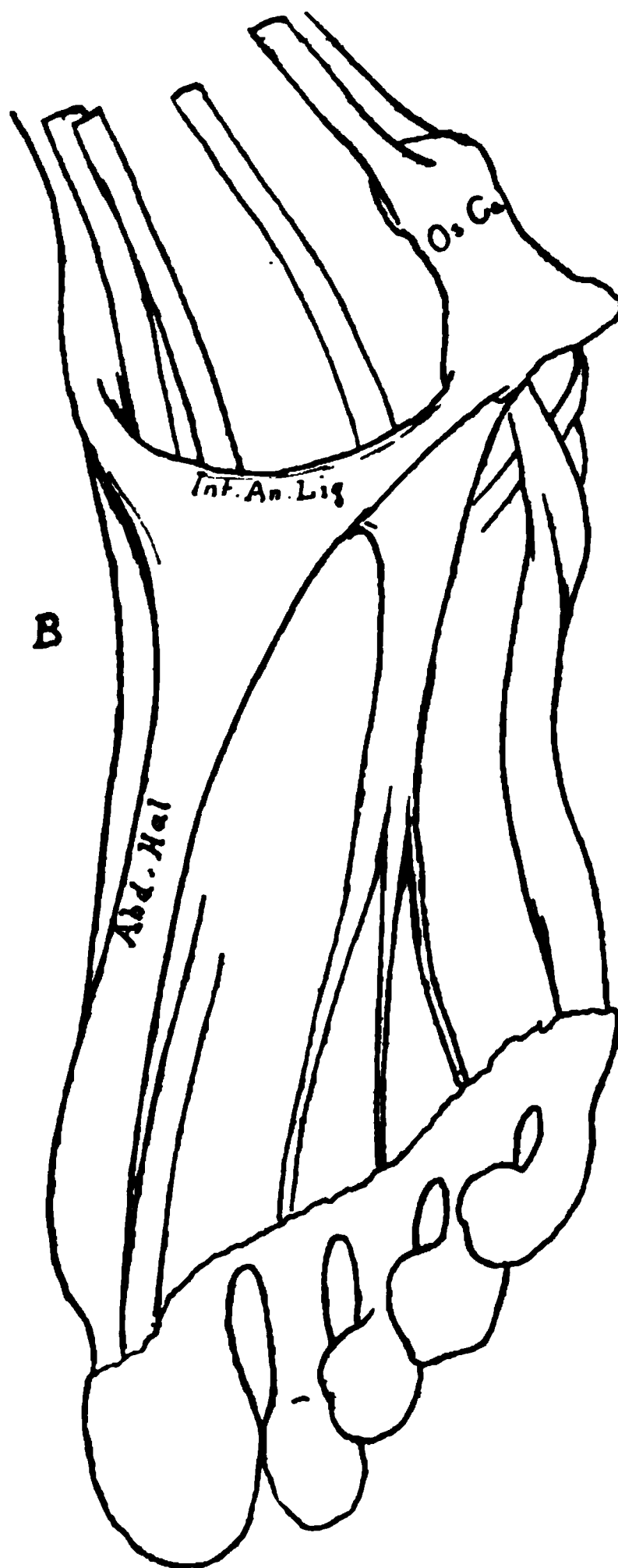


FIG. 1.

internal malleolus and the scaphoid; from this disc, fasciculi were given off to the scaphoid, cuboid, the three cuneiforms, and to the os calcis through the short plantar ligament.

The tendon of the flexor longus digitorum was displaced inwards toward the internal malleolus, while that of the flexor longus hallucis followed the displaced os calcis to which it was bound in a deep groove by its sheath. It did not groove the astragalus, and when in action tended to spring away from the bone.

The vessels and nerves occupied a position one-third of the way from the tuberosity of the os calcis to the internal malleolus.

The peroneus longus lay in a deep groove in the os calcis, going directly from that bone to its insertion in the base of the first metatarsal only, without coming in relation with the cuboid at all. As it turned beneath the os calcis, it sent a slip to the flexor brevis minimi digiti and the interossei of the fourth space. The peroneus brevis also grooved the os calcis, and was inserted into the base of the fifth metatarsal bone without coming into relation with the cuboid. The tibialis anticus grooved the internal surface and the mid line of the internal malleolus, and was inserted without coming into relation with the navicular.

The extensor longus digitorum was normal, the brevis atrophied.

The lateral ligaments of the ankle were atrophied, and the external malleolus articulated with the os calcis. The internal articulated with the navicular.

The tarsal ligaments of the dorsum were well developed, though stretched, as can be well seen by reference to the specimen.

The long plantar ligament could not be made out; the short plantar was almost normal, and the calcaneo-navicular was absent, the head of the astragalus being supported by the os calcis directly. The interosseous ligament, between the os calcis and the astragalus, was also replaced by fat.

The lower third of the tibia is round in section, and the crest is absent. The internal malleolus is blunt, and has a smooth facet inferiorly for articulation with the navicular. The external malleolus is also blunt, and articulates directly with the os calcis.

The astragalus was strongly extended, and rotated inward. The bone is flattened from above downward, the superior facet extending backward and ending in a sharp edge at the border

of the inferior surface. The posterior surface is thus absent. On the inferior surface, the posterior facet only is present for articulation with the os calcis. The interosseous groove is absent. The head and neck form an angle of sixty degrees with the body.

The os calcis is also flattened from above downward. Its external surface is convex from before backward and deeply grooved for the peroneal tendons. The external tubercle projects outward, and is very prominent; the posterior surface is long from above downward and very narrow; it is directed backward and inward. The tendo Achillis is attached to its upper and outer border, the anterior surface looks inward, and articulates with the cuboid only, although it is in contact with the fifth metatarsal.

The superior surface is narrow behind; the interosseous groove not discernible, and the posterior facet is large, with long diameter forward and inward; it is fused with the inner part of the anterior facet, the outer part being absent. The anterior part of the bone was directly beneath the astragalus, which it supported.

The inferior surface is short antero-posteriorly, being almost as broad as it is long. The sustentaculum tali is represented by a rounded tubercle separated from another directly behind it by a groove in which lies the tendon of the flexor longus hallucis.

The navicular has its long axis directed from before backward and downward, the tubercle is flattened, and articulates with the internal malleolus, being in a direct line with it.

The cuboid was displaced inward, and is flattened from before backward; its superior surface is prominently convex; the external surface is represented only by a ridge; the inferior surface is very small, and shows a sharp tuberosity, but no ridge and groove for the peroneus longus.

The metatarsal bones present no alteration except the fifth, which has a very long tubercle, the increased size being due probably to the irritation of the body-weight which it had to carry.

To sum up these changes, we find that the main deformity is at the ankle and mid-tarsal joints, and consists at the latter of a subluxation of the bones of the second row around the head

of the astragalus, thereby rotating inward, and inverting the front part of the foot. At the ankle joint, the deformity consists principally of extreme extension of the astragalus and os calcis.

The two bones most affected are the astragalus and the os calcis.

In the normal adult astragalus, the angle at which the neck joins the body is about thirteen degrees, measured as in the drawing (fig. 2, A). In this case the angle is sixty degrees, as

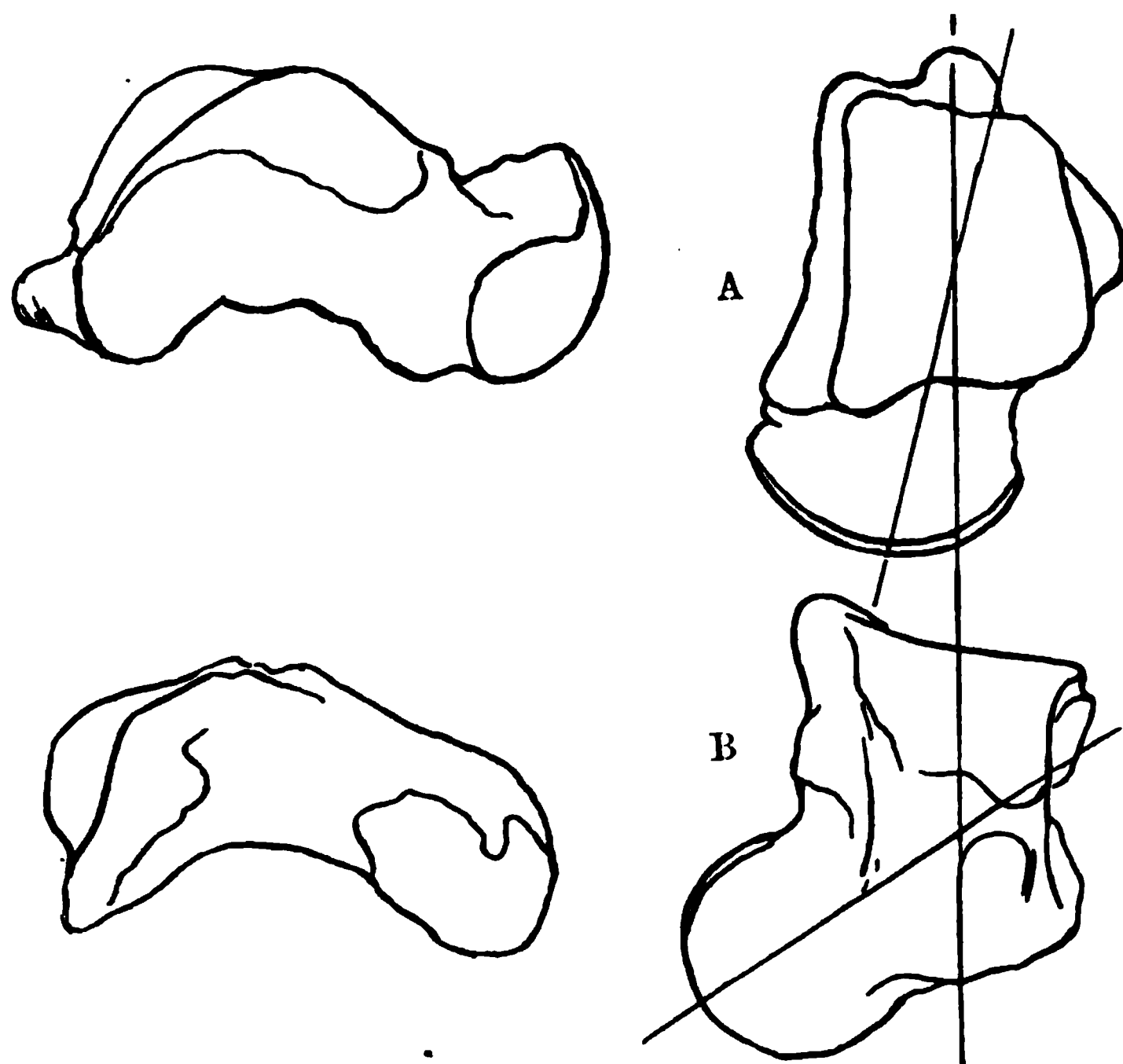


FIG. 2.

seen in fig. 2, B, besides the downward deflection. This presents an insuperable obstacle to the replacing of the foot. The effect of these bony changes is seen in the dislocation of the tendon beds, or the dislocation of the bones and tendons may have occurred at the same time, each increasing the other.

The generally accepted theory as to the cause of this congenital deformity is malposition during foetal life, while its

increase after birth is accounted for by the pulling of the tendons in faulty directions on the displaced bones, and later on, the weight of the body in walking and standing.

To go further back even than these causes, we may find an explanation in a reversion to the simian type.

In the quadrumana, the ability to invert the foot is very marked at birth, and remains throughout life; and on examining the astragalus of an adult chimpanzee, we find as normal the condition found in that from a talipetic human foot, viz.—

C

D



FIG. 3.

great obliquity of the neck to the body. In this drawing (fig. 3, D), the angle is about forty degrees. In the foetus at full term, the angle is usually about thirty-five degrees, while in the drawing fig. 3, C, it is only thirty degrees. In the human astra-



galus the angle is gradually lessened up to the normal adult extent of twelve degrees, by the continual eversion caused by walking and standing. As the bones become ossified and the ligaments set, the power of inversion becomes more and more limited. In talipes this power becomes increased and the foot fixed in this position by the contraction of the ligaments and the moulding of the bones from pressure in standing and walking.

As talipes is more frequently found in foetuses having other signs of imperfect development, such as spina bifida, cleft palate, and in monsters, this theory, which was first worked out by Parker in 1887, is plausible for the great majority of cases, and if not conclusive, is at least in accord with the accepted views on evolution.

TENTH REPORT ON RECENT TERATOLOGICAL LITERATURE. By BERTRAM C. A. WINDLE, D.Sc., M.D., F.R.S.,  
*Professor of Anatomy in Mason University College, Birmingham.*

[The author of this report will feel greatly obliged if writers on teratological subjects will supply him with reprints of their papers for use in the preparation of future reports.]

I. EXPERIMENTAL.

BERTACCHINI (i.) in his paper deals with the question as to the part played by the *blastoporic rim* in the development of the embryo, and has experimented on the ova of *Rana esculenta*, the blastoporic rim of which he punctured at various points with a red-hot needle. His conclusions are as follows:—(a) All the rim of the blastopore, when it has a diameter not greater than  $\frac{7}{10}$  mm., is embryogenic. Its anterior, lateral, and posterior regions form the cephalic, lateral, and caudal regions of the neural laminae. Its right side corresponds to the right medullary fold, its left to the left, the middle of the dorsal lip to the cephalic point of union of the folds, and the middle of the ventral lip to the region of the neurenteric canal. (b) A lesion of the anterior region of the rim stops the formation of the cephalic part of the neural crest, but does not affect the development of its caudal portion, which seems to show that the cephalic portion does not exercise any effect upon the progress of the remaining part. (c) A lesion of the middle of the ventral lip of the blastopore produces a caudal spina bifida, and alters the region of the neurenteric canal, but does not modify the formation of the dorsal and cephalic zone, nor appreciably affect the increase in length of the embryo. From this we may conclude that no zones of accretion, from which new metameres are formed from behind forwards, exist in this situation. (d) These experiments seem to bear out the concrescence theory of His. O. HERTWIG (ii.) has a paper on the effect of *centrifugal force* on the development of the ova of *Rana*. The tubes containing the ova were fixed along bars, so as to be capable of rotation through circles with radii varying from 14 to 40 cm. When the centrifugal force was exerted to a moderate extent upon the ova of *Rana esculenta*, the lighter and heavier portions of the ova became sharply separated from one another, and the process of segmentation was confined to the animal pole. In further process of segmentation the ovum departed widely from its normal type, dividing rather mero- than holoblastically. The effect, then, of the centrifugal force is to change entirely the character of the fission. The ovum is divided into unsegmented yolk, forming from  $\frac{1}{2}$  to  $\frac{2}{3}$  of the whole, and an overlying embryonic area with segmentation cavity. The resemblance to the meroblastic ovum is pushed so far that under this area a special sheet of merocytes, a yolk syncytium, is formed. BARFURTH (iii.)

states that the *cauda bifida* of amphibian larvæ can be produced by wounding the notochord of the tail. The wounded part continues to grow, but at the site of the wound a second tail is formed by regenerative budding. Each tail encloses a notochord, caudal artery, striped muscle, and, as a rule, a spinal cord. The latter is connected only in the dorsal limb with the persistent spinal cord, out of which it has been formed by regeneration. The spinal cord of the ventral limb of the tail is the peripheral portion of the original spinal cord, separated by the operation. This portion continues to grow in a normal manner. Thus the condition of cauda bifida is not a form of incomplete double monstrosity, nor does it depend upon the formation of the tail from right and left anlagen, but is an independent phenomenon of regeneration set up after an injury. The same writer (iv.) describes in another paper a remarkable larva of *Petromyzon* which had three tails, each containing a spinal cord, a notochord, and a caudal artery, as also myomeres and integument. From the experiments detailed in his first paper he thinks that two of these tails arose as the result of a regenerative process after some peculiar injury. FÉRÉ (v.) has tried the experiment of incubating eggs which had been exposed to the vapour of alcohol. The result was retarded development and the production of malformations. A period of rest between the exposure to the vapour and the incubation seemed rather to increase the number of malformations than to diminish it. Sometimes, however, in these eggs embryos have been found in a more advanced state of development than those in the control eggs, a new example of the tendency to variation, which shows itself at one time in precocity, at another in delay, or, again, in malformations, always under the influence of the same disturbing factor.

## II. GENERAL.

CORONADO (vi.) narrates a case of a *hemi-ectromelic fœtus* with eventration and anencephaly, the defects in which he traces to the fact that during her pregnancy the mother was at Manzanillo whilst that place was being subjected to bombardment. LEWIS (vii.) deals with this subject of *maternal impressions* in an essay in which he considers a number of cases which have been put forward as proving its existence. He dismisses the hypothesis as contrary to scientific evidence, and unnecessary. KOLLER (viii.) narrates a case of complete *transposition of the viscera* in a female aged 31, whose early history was unfortunately unknown: the right lung had two lobes, the left four; the heart and its chambers were fully reversed. The liver, which was very large, lay to the left, and the spleen and stomach to the right. The uterus and ovaries were normal. In his thesis the author considers the relation of this condition to double monstrosity, and points out it is not a constant accompaniment of duplicity, as Förster thought. He discusses the question of double monstrosity generally, and concludes that it may arise (a) as a result of an abnormal quality of the sex-products, whether ovum or spermatozoon; or

(b) through external influences on the sex-products during or after fertilisation. These external agencies lead most commonly to polyspermia, and thence to the production of multiple forms. LAMOURoux (ix.) gives an account of a pseudencephalous foetus in which there was also complete *transposition of the viscera*. BARBARIN and DEVÉ (x.) give an account of an infant with ectopia vesicæ and other malformations, by far the most important of which was an *anterior fissure of the vertebral column*. The cleft, which also affected the posterior aspect of the column, existed in the fourth and fifth lumbar, and all the sacral vertebrae. Fibrous bands passed across the anterior fissure and prevented the exit of any rachidian fluid. DOLÉRIS (xi.) adds a tenth to the recorded cases of *spina bifida co-existing with prolapsus uteri*. There was also talipes equino-varus. When the child cried, the cervical portion of the uterus protruded from the vulva. The bladder was in its normal position. (See the eighth of these Reports, No. xlii.) BERTACCHINI (xii.) has a long and interesting paper on an embryo of six weeks, which had *anencephaly* and lumbo-sacral spina bifida. No eyes nor ears were visible. The relation of the defects to the question of the formation of the foetus from the rim of the blastopore, as alluded to in the notice of another paper by the same author, is discussed. JOHANNESSEN (xiii.) deals with the subject of *chondrodystrophia foetalis*, a condition which has been alluded to in previous reports. The infant in this case survived two months, a rather unusual occurrence. The epiphyses of the long bones were much swollen and deformed. A description of the microscopic condition of the epiphysial cartilages is given. The condition, the author agrees with other authorities, has nothing to do with foetal rickets, from which it is distinguished by several features; nor is the disease the same as osteogenesis imperfecta. The thyroid gland was carefully examined, but showed no deviations from the normal. JOACHIMSTHAL (xiv.) narrates *another case of the same kind*, in which the child, living when the paper was written, had attained the age of eleven years, and was very intelligent, though small, growth having ceased at the age of 3. A study of the skeleton by means of the Röntgen rays showed marked proliferation of the cartilaginous ends of the bones, with almost complete absence of ossification. There was a rickety rosary, but the condition was quite distinct from that of rickets and from cretinism. CARUSO (xv.) details a similar case, which he describes as one of *foetal rickets with lymphangeiectasic elephantiasis*, in a six months foetus. It had a large head, small contorted limbs with enlarged epiphyses, spina bifida with dorso-lumbar lordosis, and lumbar kyphosis. The lymphangeiectasic condition existed at the back of the head and spine. The microscopic examination of the limb bones showed complete absence of true osseous tissue, with an osteoid structure in its place. It appears that in 1841 Otto described a case with a similar concurrence of osseous and lymphatic defects. HÉSTLE (xvi.) gives the history of a mulatto woman whose first, fourth, fifth, and sixth pregnancies all terminated by the birth of *phocomelous children* with absence of external ears. There is here imported quite gratuitously the effect of maternal impression. MAINZER (xvii.) narrates a remarkable case of *elephantiasis congenita*,

which, unlike all earlier cases which are of dropsical lymphangiectasia or of telangiectasia nature, exactly resembled the true acquired elephantiasis arabum. It affected the extremities and the external genitalia. MANOUVRIN (xviii.) records observations on several *dwarfs*. The first of these had grown 3 cm. in the twenty months succeeding his twenty-third and a half year, another proof of the protracted period over which the growth of dwarfs sometimes extends. The second (Delphin Sirvoux), æt. 15, measured 0.991. The arrest of growth had occurred some time after birth, and was therefore unaccompanied by microcephaly. The third dwarf (Princess Blanche), æt. 23, was born of normal parents, and was of the usual size at birth. Arrest of development commenced very shortly after birth. Her stature (1.24 m.) is that of a child of eight to nine years. The breasts were of good size; she menstruates, but the pubes is quite destitute of hair. REBOUL (xix.) describes a *hairy man* whom he saw exhibited at the fair of Nîmes. He was of middle height, strong and well-shaped, and aged 45 to 50. His hair was 37 cm. in length, and that of the beard measured 27 cm. The front of the trunk was covered, especially at the middle line, with black hairs from 4 to 5 cm. in length. The back was still more hairy, the central line being especially thickly clad. The lateral portions of the back, the shoulders, and the limbs were also well covered. As in most similar cases, there were various dental anomalies, hare-lip, with a grooved, but not perforated palate, and ill-set teeth, the incisors being placed transversely. VAN DUYSSE (xx.), in a description of a case of *cyclopia*, agrees with Dareste that the fusion of the eyes takes place always along the line of the choroidal fissure, the juxtaposed clefts being confluent over a greater or less extent. JACCARD (xxi.), in a paper on monsters in the organic world, deals generally with the production of variations by artificial means and the causes of abnormalities.

### III. DUPLICITY.

FÉRE (xxii.) contributes a second note on the development of embryos in *double-yolked fowls' eggs*. (An account of the former series of experiments will be found in the eighth of these Reports, III. i.) In three cases there was no development. In five only one embryo developed, the two yolks adhering to one another. In seven instances an embryo developed on each yolk, and of these, in three cases both embryos were normal. In three other cases there was one normal embryo. On the other yolk, in one egg was a blastoderm without visible embryo; on a second, a double monster of the syncephalous type; and on a third a cyclops. The remaining egg had an omphalocephalic monster on one yolk, the other bearing a blastoderm without embryo. IMMERMAN (xxiii.), from a further series of examinations of *double-yolked eggs*, concludes that (a) there are two kinds of such eggs, those in which there is a common vitelline membrane for both yolks, and those in which each yolk has its own vitelline membrane; (b) there is no normal position for the twin embryos derived from such

yolks; (c) in the process of development one yolk and the embryo which it bears suffers from the influence of the other; (d) eggs of this kind, with separate vitelline membranes, may arise from the simultaneous rupture of two follicles or from the presence of two ova in one follicle. Those which have a common vitelline membrane apparently come from a single follicle; (e) two ova may sometimes be found in a single Graafian follicle in man. HERRICK (xxiv.) describes a case of *ovum in ovo*. The hen's egg in this case contained a small included egg, possessing a hard shell, a shell membrane, and a small yolk. This included egg lay in the yolk of the larger, and not in the albumen, in which respect this case is stated to be unique. He also describes a second case in which the included egg lay, as usual, in the albumen of the larger egg. The remarkable cases of this nature may be thus classified.

I. Enveloping egg usually normal, but occasionally of large size; blastoderm recorded in at least one instance.

Enveloped egg:—

- (a) In yolk; small; composed of shell, shell membrane, albumen, and yolk; no blastoderm known to occur in this or in the following variations; single case recorded above.
- (b) In albumen; small; composed usually of shell, shell membrane, albumen, and rarely with yolk; few cases recorded.
- (c) In albumen; small; usually with shell, shell membrane, and albumen, but no yolk; most cases of *ovum in ovo* reported are of this kind.
- (d) In albumen; usually small and variously distorted, so as to bear little resemblance to an egg at all.

II. Enveloping egg of colossal size; complete; blastoderm probably present.

Enveloped egg:—

- (a) Without shell, but otherwise complete. In this case a common shell may surround two or three eggs complete except for shells and shell membranes; forming 'double-yolk' or 'triple-yolk' eggs.
- (b) One of the enclosed eggs of normal appearance and size, possessing shell, albumen, and yolk; the other eggs surrounded by a common shell, but having no shells of their own.

In the opinion of several writers the small included egg represents a fragment of a normal ovum which has been ruptured, and thus has parted with some of its substance after leaving the ovary. This fragment is then treated in the oviduct like a full-sized egg. The small egg-like body thus produced is sometimes laid, but occasionally it is driven by antiperistaltic action up the tube until it collides and fuses with the mother egg. This theory will suffice to explain the first class of inclusions on the supposition that rupture takes place in the upper part of the oviduct, or at least after the first layers of

albumen have been added to the normal egg. Since the small included eggs are generally yolkless, we must infer that such ruptures are, as a rule, confined to the albumen. The theory of yolk-rupture will not, however, explain the second class of abnormalities, such as double or triple yolk eggs. We have here a case of fusion of the albumen in two or more ova, which are treated in the uterus as one egg and surrounded by a single shell. This process is sometimes complicated by the inclusion of a third egg of normal size and already covered by a hard shell. These conditions may be brought about by irregularities in the mechanism of the oviduct, as when any given egg does not receive its shell and is not laid before it encounters others coming down the oviduct at the same time. WYLIE (lxiii.) has met with a case of *included fetus*, which was removed by operation from the lesser peritoneal cavity of a child æt. five months. The parasite consisted in part of imperfectly-formed viscera, two limb buds projecting from the mass.

SCHULTZE (xxv.), in a discussion as to the *origin of double monstrosities*, thinks that this result may follow from three possibilities:—(a) The ovum escapes from the ovary with two nuclei. These may be fertilised by two spermatozoa from which two processes of segmentation would follow. Here the duality of the ovum is determined in the ovary. (b) Through over-ripeness, the innate tendency to division on the part of the ovum may lead to its division into two equal or nearly equal parts, each of which may subsequently be fertilised. Here the ovum divides abnormally shortly before fertilisation. (c) The ovum may be normally fertilised and proceed to the first division. Then, by some unknown process, the same result may follow as that which has been experimentally produced in so many different ways—that is, each segmentation sphere may go on to an independent development. Here the abnormal division takes place after the first process of segmentation.

WRIGHT (xxvi.) describes a case of twins, both being affected with *syringo-myelia*. Both were hydrocephalic. (In connection with this the reader may be referred to a list of cases of similar malformations in twins given in a paper by the reporter in this *Journal*, vol. xxvi. p. 295.) EUSTACHE (xxvii.) gives an account of a case of *Janiceps* in which the cranium consisted of twelve bones, viz., two occipitals, four temporals, one frontal, and one sphenoid. One of the faces had one inferior maxilla, two superior maxillæ, two malars, and two palates. The other, which was very incomplete, had only two superior maxillæ. The brain had a single mesocephalon. THOMPSON (xxviii.) narrates a case of *triplets* in which one child, a male, was normal, and had its own placenta and membranes. Along with it was born a thoracopagus double monster of the female sex. OPITZ (xxix.) has described a case of *acardiacus*, in which there were rudiments of both legs, the left arm, and the external genitalia. The greater part of the intestine lay in a large umbilical hernial pouch. On the upper aspect of the trunk lay a flaccid body which contained the eyes, fused into one, and the rudiments of a mouth. SCHIEDMACHER (xxx.) describes two further cases of *acardiari*, one of which was headless, the other



having a rudimentary head. In the last volume of this *Journal*, the present reporter has a paper on *Epignathus* (xxxi.) in which the theory is put forward that forms of double monstrosity of this kind may be due to the imperfect development of a portion of germinal substance, or perhaps even of a polar body. Since this paper was written he has received a reprint of MARCHAND's article on malformations, in which he finds that a similar view has been independently expressed (xxxii.).

#### IV. HEAD AND NECK.

MANOUVRIER (xxxiii.) gives a careful description of the *brain of a deaf mute*, in which there were very considerable departures from the normal condition in the right Sylvian region. V. MONAKOW (xxxiv.) gives a full description of a case of *microcephaly*, the subject being a child aged  $2\frac{1}{2}$  years who had never been able to suck. The chief interesting features in the brain were microgyry, with quite atypical, though medullated, bundles of fibres in the cerebrum. There was heteropy of the grey matter there and in the medulla oblongata, the inferior olive being abnormally related to some of the fibres of the eighth nerve. BOUCHACOURT (xxxv.) describes a case of *frontal encephalocele*, which had prevented the union of the nasal processes. As secondary conditions were present, abnormal separation of the orbital cavities, bifid nose, and median hare-lip without cleft of the palate.

KOISTER (xxxvi.) narrates a case of *multiple canals in the spinal cord*, observed in the embryos of *Sterna hirundo* and *Larus canus*, a series of sections showing the presence of two canals, one dorsal and larger, the other and smaller being ventral. SENATOR (xxxvii.) gives *another case* in which the central canal was in part double, in part triple. In addition to this there was a heterotopic mass of grey matter near the posterior cornu of the brain, which consisted of ganglion cells, like those of the posterior cornu, of neuroglia corpuscles, and of some medullated fibres. CUTORE (xxxviii.) gives a further instance of *multiple central canals* occurring in the chick embryo of forty-eight hours' incubation. The primary and normal canal persisted throughout, but in addition there were in parts of the cord several other canals of more or less extent, lined by epithelium of normal appearance. (For another paper on this subject, cf. *Anatomischer Anzeiger*; xv. p. 56.) LENOBLE and CIVEL (xxxix.) describe a case of *congenital dermoid cyst* of the neck, which lay near the hyoid and base of the tongue. This they believe to have been a case of foetal inclusion. A still further advanced *teratome* is described by BRUNKER (xl.) in a baby of two months old, from which the tumour had to be removed on account of its rapid growth. It extended from the zygoma to the third rib. On microscopic examination it was found to contain embryonic brain tissue, fat, cartilage, striated muscle, glands, cysts, and the rudiment of an eye. A third example of *cervical Teratome* is described by HAGENBACH-BURCKHARDT (xli.),



occurring on the right side of a child of three weeks old, from which it was excised. It contained cartilage, fat, and neuroglia. It possessed a number of cysts, lined by flattened columnar or ciliated epithelium. One of these cysts contained hair. A *congenital cyst of the base of the tongue*, demonstrated by JOHNSON (xlii.), is less easy to classify. It occupied the extreme posterior part of the tongue, lying in the middle line and projecting on the surface as a smooth hemispherical swelling. It was lined by a layer, in most parts several cells thick, of flattened epithelium, and contained what was apparently coagulated mucus. RUFFINI (xliii.) describes a semilunar bony eminence projecting from the postero-inferior portion of the mastoid process in some human temporal bones. It is hollow, and connected with the mastoid cells. He looks upon it as the morphological equivalent of the bulla tympani in other mammals. FRASSETTO (xliv.) describes a *parietal suture* in a skull of *Simia satyrus*, whose line ran obliquely across the bone from near the junction of the sagittal and lambdoidal sutures towards the stephanion. It was only visible on the outer surface of the cranium, and had a Wormian bone at its lambdoidal end. (This suture is known as a rare anomaly in the human skull, but so far as the reporter is aware, has not been previously observed in any anthropoid cranium.)

GROSHEINTZ (xlv.), in a paper on *Hypsistaphyly and Leptoprosopy*, notes the frequent combination of the latter condition with a high, small palate. Small orbits and nasal apertures also, he says, accompany high palate. BROECKART (xlvi.) gives some curious *anomalies of the soft palate*. In the first, the anterior pillars of the pharynx were completely separated from the rest of the lateral wall by a deep cleft. In a second case this condition was observed on one side only. In neither case was the condition due to tonsillitis. In a third case he records congenital perforations of the soft palate. He regards these as aplasic phenomena, defects of formation due to some vascular anomaly in early foetal life. VAN DUYSE (xlvii.) describes the fused pair of eyes of a *rhinocephalic* monster, each pupil having a coloboma. The clefts were prolonged backwards to the rudimentary optic nerve, which was no doubt formed by the fusion of the two normal nerves.

V. HIPPEL (xlviii.) describes a case of *hydrophthalmus congenitus*, in which there was marked expansion of the cornea and corneo-scleral zone, deepening of the anterior chamber, complete or nearly complete absence of Schlemm's plexus, signs of former irido-cyclitis, parenchymatous keratitis with marked swelling of the corneal substance, with presence of an internal ulcer of the cornea. There was ectropion of the pupillar border, and the lens was very small. The zonula was much stretched and hypertrophied, the papilla was deepened, and the lamina cribrosa displaced backwards. In the left eye there was also a coloboma iridis.

VAN DUYSE (xlix.) gives a most detailed account of the condition of *cryptophthalmus* exhibited by a child, the literature of the subject being very fully dealt with. In the case in point both eyes exhibited evident traces of inflammation. As an appendix to this case an account

of an instance of unilateral anophthalmus occurring in a pigeon is given. The same writer (1) has a paper on *congenital anophthalmus*, of which condition he has only been able to find five cases proved to be genuine by a microscopic examination. To these he now adds a sixth. The child, which was seen by him at the age of three days, died when three months old. There was no optic nerve nor chiasma, nor tract, and the corpora quadrigemina, especially the anterior, were badly developed. There was no external geniculate body, nor brachia conjunctiva. A series of sections of the whole orbital cavity was made, which demonstrated the presence of muscles and nerves. The eyeball was, however, reduced to a small nodule, measuring 1 mm. in diameter and 5 mm. in length, which was composed of a fibrous envelope clothing a choroid, whose vessels filling the central cavity of the nodule, were separated from one another by branched pigmented cells.

NUEL (li.) records two *malformations of the lens*. In the first the child, aged 4, had a microphthalmic eye, in which the lens was very small and perforated in the centre by a fibrous growth, which covered that portion which rests in the fossa patellaris. In front this growth projected through the pupil. The ciliary body was small and atrophic. In the second case the child, æt. 14, had a persistent hyaloid artery. The lens was small and displaced anteriorly and to the nasal side. It adhered to the posterior surface of the cornea. Here also the ciliary body was in a very atrophic condition.

VAUGHAN (lii.) adds another to the list of cases of hereditary persistent *branchial clefts*. In the case in question, that of a woman, the clefts, or fistulæ, were in the most common site, viz., about half an inch above the sterno-clavicular joints. Four members of the family, all female, in three generations have been known to possess the same abnormality. These were (a) the grandmother of the patient, who had one fistula on the right side of the neck; (b) the patient as above; (c) another granddaughter, with one fistula on the left side of the neck; (d) a great-granddaughter similarly affected to the last.

## V. THORAX.

STOYANOV (liii.) has a lengthy and exhaustive thesis on the whole question of *polythely and polymastia*, in which a number of new cases are described and the literature of the subject fully dealt with. The author agrees with the views of Schmidt as to the origin of the condition, which he believes to be quite the reverse of rare. (For Schmidt's view see the eighth of these Reports, No. xxix.; cf. also Burckhardt, Report IX., No. xlviii.) He agrees that the condition is hereditary and atavistic. TEMPLETON (liv.) records a case of *axillary mamma*, which had no nipple, but a small central pore, at the point of the attachment to the skin, from which pore could be expressed, during lactation, a fluid with all the physical and microscopic characters of milk.

LEVY (lv.) describes a case of absence of the pectoral muscles of the

right side with *deficient formation of ribs*. The third rib cartilage was a little stump about half an inch in length, and the fourth a narrow curved strip  $2\frac{1}{2}$  inches long, lying close along the upper border of the fifth cartilage. The end of the curtailed third rib could be obscurely felt in the axilla just under the margin of the pectoral muscle and lying close to the second rib, while the attenuated termination of the fourth rib was found a little further back in the axilla. POPOWSKY (lvi.) gives several cases of *ribs bifid* at their sternal extremities, a condition which, taking into consideration the fact that the anthropoids have thirteen pairs, of which eight are connected with the sternum, he believes to be atavistic.

FISCHER (lvii.) describes an *extra lobe of the right lung* situated at its upper part, round which the vena azygos major wound instead of round the right bronchus. CIVETTE (lviii.) records a case in which there were only *two aortic valves*, which were placed, the one anterior, the other posterior. The pulmonary artery had the normal number. There was no communication between the right and left hearts, but during life there was present a condition of extreme cyanosis. DURANTE (lix.) gives a case of *transposition of the great vessels* of the usual type.

DÉVÉ (lx.) gives three cases very similar to that of Fischer (*supra*) in which the azygos vein cut off an accessory lobe from the upper part of the right lung. (This is a sufficiently well-known anomaly; the azygos vein is really embedded in a deep groove in the lung.)

## VI. ABDOMEN.

BERTINO (lxi.) narrates an interesting case of *eventration* which, as he points out, must have occurred after the closure of the abdominal wall, and cannot therefore be accounted for by the usual theory of an arrest of development. An opening existed in the right half of the anterior abdominal wall, about the level of the umbilicus, through which opening projected a bundle of abdominal viscera, with no membranous covering. The opening in question was nearly circular, and measured 4 cm. in diameter. It was separated from the umbilicus by a tract of ordinary abdominal wall. The bundle of viscera consisted of œsophagus, stomach, duodenum, small intestines, and parts of the colon. The umbilical vein passed in the superficial part of the abdominal wall along the edge of the opening. Passing through this, it made its way to the liver, where it had a normal distribution. SCHAUTA (lxii.) has recorded a case of *diastasis of the symphysis pubis*, which is almost certainly congenital, and which, being unaccompanied by ectopia vesicæ, is unique. The separation between the bones was to an extent of 2 cm., their ends were rounded, and there was no history or evidence of any disease of the joint. SIEVERS (lxiv.) describes a case of congenital *hour-glass stomach* in a woman æt. 38. There was a tube-like connection between the two portions of the stomach, which was so small as only to permit the passage through it of the little finger. LARDENNOIS (lxv.) has recorded a case

of *duodenal stenosis* occurring in the adult, but, as he believes, of congenital origin, a view which he considers to be established by the microscopic examination.

LETULLE (lxvi.) has met with two cases of *duodenal diverticula*, small pouches existing around the diverticulum Vateri. In a third case he describes a single *diverticulum of the œsophagus* situated on anterior aspect, and 12 cm. above the cardiac orifice.

BRADLEY (lxvii.) describes a case of *atresia ani* with recto-vulval fistula, which he met with in a sheep. The animal lived to the age of 7½ months. The rectum opened into the urino-genital sinus. The same author (lxviii.) has contributed a second case of the same kind during the year. PHISALIX (lxix.) narrates a case of complete *absence of the inferior vena cava* in a guinea-pig, the place of the missing vein being taken by a persistent left cardinal vessel.

CHEYNE (lxx.) records a case of a *third kidney* which lay a little below the normal right organ, and had its own ureter and blood supply.

## VII. GENITALIA.

KELLOCK (lxxi.) has met with two cases of complete *hypospadias* with cleft scrotum, occurring in a family of nine children, all the rest being normal. LANGE (lxxii.) records a remarkable case of *double penis*. The two organs lay side by side; there were two scrotal cavities each with a single testis. There was no patent anus, but from either scrotum there led down to the perineum a raphé. Each of these terminated in the anal region at a small button-like skin appendage. There were two bladders, each with a ureter opening into it. The two cavities were quite separated from one another, and the right was the larger of the two. There were two urethræ communicating with one another, one prostate and two vesiculæ seminales. The rectum opened by narrow passages into either urethra. There were no signs of duplicity in the skeleton. (For former cases of diphallus, see Report VI., Nos. xxviii. and xxix., and Report VIII., No. xli.) NAGEL (lxxiii.) deals with the question of *hermaphroditismus verus* in connection with a case described by Blacker (*Tr. Obst. Soc. Lond.* xxxviii.). V. WINCKEL (lxxiv.) has compiled a most valuable account of the various malformations of the female generative organs, which he arranges chronologically, according to the order of their occurrence during development. To this classification is added a number of cases observed by the writer himself. LESSER (lxxv.) records a case of *double uterus with cloaca*. The patient (not a virgin) had a normal clitoris, labia, and urinary meatus. Behind the latter were the openings of two vaginæ, separated by a thin septum. Each had possessed a hymen, and that of the left side was intact. Posteriorly to these was another thin septum, behind which was the anal opening. Behind this again was the posterior commissure. Examination revealed the fact that there were two perfect vaginæ and two uteri. There was a patch of pigment at the normal site of the anus.

ULLRICH (lxxvi.) places on record four cases of *malformations of the female genitalia*: (a) Uterus duplex bicornuatus, with separate vaginae; (b) almost complete absence of internal genitalia, with total absence of vagina; (c) uterus unicornuatus, with absence of right annexæ; (d) uterus infantilis. CIVETTE (lxxvii.) records a case in which there was *absence of vagina*, an infundibulum 2 cm. replacing it. There was a supernumerary ovary on the right side. A very small uterus was connected with the left tube, but the right tube failed to reach it. Both tubes were patent only in their upper parts.

MUNDÉ (lxxviii.) has an article on *deficiencies of the female genitalia*, with numerous illustrative cases and references to the literature.

WIART (lxxix.) records a case of *hernia of the Fallopian tube* into the inguinal canal in a new-born child. This is said to be a rare condition, Schultz (*Thèse de Paris*, 1897) having only been able to collect twelve cases of it, but the author has observed a second instance also in a new-born child. NEUGEBAUER (lxxx.) narrates a remarkable case of a *second clitoris*. A young woman, just delivered of her first child, was being examined as to her fitness for a position as wet-nurse, when the following conditions were observed:—The genitalia and clitoris were normal, but springing from the middle of the perineum was an organ 1 inch in length, of the size and shape of a penis, with a perfect glans and a partial prepuce. On manipulation, this erected itself to a length of 2 inches, and was then as thick as a little finger. It was solid, and there were no signs of testicles or other abnormal structures in the neighbourhood. The extra clitoris was provided with two well-developed corpora cavernosa, one of which could be traced to the ramus of the pubes.

### VIII. EXTREMITIES.

BARWELL (lxxxix.) recorded at the Pathological Society of London a case in which the *right hand and forearm were wanting*, being represented only by a fleshy prominence bearing minute nail-buds. He regarded the condition as one of early arrest of development, due to the influence of the nervous system. In the right lower limb the femur and thigh were absent. In the discussion which followed, Mr SHATTOCK stated that he believed that Weissmann's views afforded the best explanation of this class of malformations, an irregular distribution of determinants being the cause of the defect. WALLENSTEIN (lxxxii.) notes a case of *peromelia*, in which there were no upper extremities. In the lower extremities the tibiæ and fibulæ were absent, the feet articulating directly with the femora. DURLACHER (lxxxiii.) gives a series of cases of *hereditary malformations of the hands and feet*. In this case the boy, his mother, and sister, all had similar defects. The mother, aged 36, had on her right hand apparently only three fingers, but really the pollex and index and the medius and annularis were completely syndactylous. The condition of the left hand was much the same, but there was more separation, as the pollex and

index possessed quite separate nails. In the right foot the great and second toes were quite syndactylous. The third, fourth, and fifth toes were syndactylous, and there was a sixth (post-minimus), quite separate. The left foot was normal. Of this woman's three children, the eldest, a girl, was quite normal. The second, a boy, had the following defects. The pollex and index were syndactylous on each hand, the end phalanges being separate on the right and rather more on the left. On the feet, right side, the first and second toes were fully syndactylous, the third was diminutive, and the fourth and fifth were partly syndactylous. On the left, the first toe was normal, the second diminutive, the third and fourth syndactylous, and the fifth separate but small. The third child, a girl, had on the right hand the pollex and index syndactylous, and also the medius and annularis. On the left, the pollex and index were webbed, and the medius and annularis syndactylous. On the right foot, the first and second toes were syndactylous, the third diminutive, and the fourth and fifth syndactylous. The left foot presented the same condition as the right foot of the mother.

STOUFFS (lxxxiv.) records a case of *deficient osseous apparatus*. The hands had three digits apiece only, and were connected with the scapulæ by a single bone, the nature of which is not mentioned; possibly it was undeterminable. The long bones of the leg were absent; a single centre of ossification represented the tarsus on either side, and the feet were perfect, save for the fact that there was a web between the fourth and fifth toes. There was double hare-lip also.

VIRDEN (lxxxv.) records a case of upward *displacement of the left scapula* in a girl æt. 10½. A similar condition is noted by PIRSCH (lxxxvi.). (This condition, which is known, from the name of its first describer, as 'Sprengel's deformity,' has been dealt with in Report VIII., No. xlviii., where references to the literature will be found.)

HULTKRANTZ (lxxxvii.) gives five cases of *defect of the clavicle*. In one instance, three daughters of a mother, herself wanting part of the clavicle, all presented an absence of the acromial end of that bone. This defect appears to be generally bilateral, and as a rule a cord-like structure stretches from the sternal rudiment of the bone to the coracoid process. The condition appears to be very commonly associated with one of deficient development of the skull.

CARPENTER (lxxxviii.) records a case of double *absence of clavicles*. In five other members of the family there were clavicular defects. In the case in point the clavicles were replaced by two small thin, tapering fragments of cartilage attached by their broader extremities to the sternum. GEIPEL (lxxxix.) adds another to the list of cases of *absent pectoral muscles*. EISLER (xc.) has examined sixty hands for supernumerary carpal elements, of which two only, both coming from the same man, presented any such ossicles. In the right there were secondary trapezoid, styloideum, and epipyramis, and in the left a secondary trapezoid.

PFITZNER (xci.) has a paper on *brachyphalangy* (cf. Report IX., No. lxxvii.). In order of frequency of occurrence, he states this occurs as follows:—(1) Terminal phalanx of the thumb; (2) middle



phalanx of minimus ; (3) middle phalanx of minimus and annularis ; (4) middle phalanx of minimus and index ; (5) metacarpal of thumb. Hyperphalangy, he thinks, should be considered as a reversion. He mentions a case in which he found a rudimentary phalanx between the middle and terminal phalanges of the third toe of an adult man. It was nearly fused with the terminal phalanx.

The same writer (xcii.) records a case of *duplicity of the fifth toe*, in which the additional member lay between the fourth and fifth metatarsals, and consisted of a single metatarsal-like bone, articulating proximally with the fourth metatarsal, and distally with the fifth. This toe, otherwise single, carried two terminal phalanges.

MAZZITELLI (xciii.) has collected 120 cases of *absence of fibulæ*. The condition was bilateral in 37·7 per cent. Of the bilateral cases, 25·6 per cent. showed complete absence ; both in the complete and partial unilateral absence the defect was more often met with on the right than on the left side. Males were more frequently affected than females.

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A PERICARDIAL SAC IN WHICH THE LARGE AZYGOS VEIN PIERCED THE SAC BEFORE OPENING INTO THE SUPERIOR VENA CAVA. By C. M. COOPER, M.B., M.R.C.S., *Junior Demonstrator of Anatomy, University of Edinburgh.*

THE variety described in this note occurred in an adult male subject dissected during the present winter in the University Practical Anatomy Rooms.

The pericardial sac was extensive, and enclosed the whole length of the ascending thoracic aorta and the lower two-thirds of the circumference of the arch of the aorta, at its upper limit blending with the outer coat of this vessel.

The origins of the right and left pulmonary arteries and the ligamentum arteriosum were included within the sac.

The large azygos vein did not open into the superior vena cava outside the sac, but after arching above the root of the right lung, it pierced the pericardium, and for the distance of an inch lay free within the sac, the included portion of the vein being invested anteriorly and laterally by the serous pericardium. It then opened into the superior vena cava one inch and a half distant from the superior caval opening in the right auricle. The superior vena cava was included within the sac for the distance of two inches.

In this specimen the left bronchial artery coursed between the left recurrent laryngeal nerve and the ligamentum arteriosum as the nerve wound round the arch of the aorta. This artery was single, and arose from the descending thoracic aorta. It entered the lung on the anterior aspect of the left bronchus.

The left vertebral artery arose from the upper aspect of the arch of the aorta, between the origins of the left common carotid and left subclavian arteries.

# Journal of Anatomy and Physiology.

## ON THE TOPOGRAPHICAL ANATOMY OF THE ABDOMINAL VISCERA IN MAN, ESPECIALLY THE GASTRO-INTESTINAL CANAL. By CHRISTOPHER ADDISON, M.D., B.S. (Lond.), F.R.C.S., *Professor of Anatomy, University College, Sheffield.*<sup>1</sup> PART II. (PLATES LII.-LIV.)

(Continued from page 586, vol. xxxiii.)

TABLE III.<sup>2</sup>

*Table of Average Relations of the Stomach to the adjoining Viscera, and accessory Tables relating thereto.*

(Compiled from Tables II., III., V., and VI. in the Appendix. All measurements in centimetres.)

### *The liver.*

|   |                 |
|---|-----------------|
| The upper border in the R.L. line as to E.F.,                 | 10·4 cm. above. |
| „ „ „ as to inf.-ster. notch,                                 | 6 cm. above.    |
| „ „ M.L. „ „ „  | 8 cm. below.    |
| „ „ „ „ E.F.,   | 9 cm. above.    |
| The left extremity of the liver from M.L.,                    | 7·1             |
| „ „ „ above E.F.,   | 7·4             |
| The extent that the liver overlaps the stomach in the         |                 |
| <sup>3</sup> plane of the left point of the lesser curvature, | 1·43            |
| The extent that the liver overlaps the stomach in             |                 |
| M.L.,   | 1·6             |
| The extent that the liver overlaps the upper border           |                 |
| of the pylorus,   | 1·8             |

<sup>1</sup> In reading this paper, reference should be made to figs. 1 and 3 and the Plates in Part I.

<sup>2</sup> For convenience, it may be repeated that R.L., L.L., and M.L. indicate respectively, the right lateral, the left lateral, and the middle lines, and that E.F. is a line drawn transversely across the body, midway between the pubes and the supra-sternal notch.

<sup>3</sup> The points are defined in the text.

*The transverse colon.*

|   |             |
|---|-------------|
| The upper border in the R.L. line as to E.F.,   | 2.25 below. |
| "                    "                    M.L.          "          "  | 3.2     "   |
| "                    "                    L.L.,     "          "  | 1.3     "   |
| <sup>1</sup> Highest 'point' of the splenic flexure of the colon as to E.F.,  | 2.9 above.  |
| Highest point of the splenic flexure of the colon from M.L.,  | 10          |
| <sup>2</sup> Outer border of the descending colon, or the splenic flexure, in the plane of E.F. (32 cases) from M.L., | 10.6        |

*The pancreas.*

|  |            |
|--|------------|
| The upper border in the middle line as to E.F.,  | 2.4 above. |
| "                    "                    "          lesser curvature,                   | .5     "   |
| The anterior          "                    "          as to E.F.,                        | 1.5 below. |
| "                    "                    "          greater curvature,                  | 1 above.   |
| "                    "                    L.L. line as to E.F.,                          | .3     "   |
| "                    "                    "          "          as to greater curvature, | 1.5     "  |
| The extent of the pancreas to the left of the middle line,                               | 9.1        |
| The extent of the stomach to the left in the same plane,                                 | 9.5        |

*The left kidney, pancreas, and greater curvature of the stomach.*

|  |                |
|--|----------------|
| The upper pole of the left kidney as to E.F.,  | 4.5 cm. above. |
| "                    "                    "          as to the upper border of the pancreas, | 1 cm.     "    |
| <sup>3</sup> The upper pole of the left kidney from the middle line,                         | 6.1 cm.        |
| The upper border of the pancreas in the L.L. line as to E.F.,                                | 3.4 above.     |
| The depth in a vertical plane of the gastric surface of the pancreas in the L.L. line,       | 3.1 cm.        |
| The depth antero-posteriorly of the inferior surface of the pancreas in the L.L. line,       | 2 cm.          |

*The left kidney and supra-renal.*

|  |         |
|--|---------|
| The 'inner point' of the upper segment of the kidney from the middle line, | 3.8 cm. |
| <sup>4</sup> The outer point of the left kidney from the middle line,      | 9.6     |

<sup>1</sup> The points are defined in the text.<sup>2</sup> In 8 cases the splenic flexure of the colon was wholly situated below E.F.<sup>3</sup> The left lateral line is practically in the vertical plane of the upper pole of the left kidney.<sup>4</sup> This is the point along the extreme outer border which is nearest E.F.

|  |           |            |
|--|-----------|------------|
| The outer point of the left kidney as to E.F.,       | . . . . . | .6 below.  |
| The lower pole                                       | „ „ „     | 6.2 „      |
| „ „ „ as to the iliac crest,                         | . . . . . | 3.3 above. |
| The lowest point of the left supra-renal as to E.F., | . . . . . | .5 „       |
| The highest  | „ „ „ „   | 5.5 „      |

*The spleen.*

|   |           |            |
|---|-----------|------------|
| <sup>1</sup> Distance to the left of the lowest 'point' of the anterior border of the spleen, | . . . . . | 11.5       |
| The lowest point of the spleen as to E.F.,  | . . . . . | 1.4 below. |
| The highest point of the spleen as to E.F.,   | . . . . . | 8.7 above. |
| The „ „ „ infra-sternal notch,  | . . . . . | 1.1 below. |
| The highest point of the spleen from the middle line,   | . . . . . | 5.8        |
| The innermost point of the spleen from the middle line,                                       | . . . . . | 3.6        |

## II. AVERAGE POSITION OF THE STOMACH IN RELATION TO OTHER ORGANS.

In this place the average position of the stomach in relation to the adjoining viscera in the whole series will be stated. It is, however, fully recognised that in some cases, especially with regard to the transverse colon, and to some less extent the liver, the mere statement of an average does not sufficiently indicate what we should expect to meet with in any particular case.

*The Liver.*—*The upper border* of the liver in the middle line is situated .8 cm. below the infra-sternal notch, and 9 cm. above E.F., passing across, that is, a little higher than the upper border of the cardiac orifice. It passes to the left, in front of the stomach, for 7.1 cm., sinking in level 1.6 cm. The left extremity of the liver is therefore situated 7.4 cm. above E.F., 7.1 cm. from the middle line; or, in general terms, 3 inches to the left of the middle line 1 inch below the level of infra-sternal notch; or behind the sixth rib near the costo-chondral junction. The summit of the stomach, on a posterior plane, projects 2.2 cm. higher than this left part of the liver.

<sup>1</sup> The anterior border of the spleen sometimes passes imperceptibly into the basal surface. The point had then to be selected arbitrarily.

The *lower border of the liver*, passing from its left extremity towards the right, sinks but little in level for its first 2 cm., after which it bends almost directly downwards, with a convexity to the left and downwards, until in the plane of the 'left point' of the lesser curvature the liver overlaps the stomach for 1.43 cm.; the margin of the liver in this plane being 5.18 cm. from the middle line, and 4.5 cm. above E.F. From this point the lower margin of the liver follows fairly regularly the lesser curvature, overlapping it in the middle line 1.66 cm. and at the upper margin of the pylorus 1.8 cm.

The lower border of the liver in the middle line is .3 cm. above E.F.; the vertical depth of its anterior surface in the middle line thus being 8.7 cm.

*The Transverse Colon.*—The upper border of the transverse colon crosses the middle line 3.2 cm. below E.F., being nearly in contact with the lower border of the stomach.

Continued to the left, in a great many cases there is a loop of colon passing, either upwards in front of the stomach, or downwards, in the interval between the middle line and the left lateral line. In the left lateral line the upper border of the colon is 1.3 cm. below E.F. in contact with the lower border of the greater curvature of the stomach, having risen 2 cm. in level from the middle line. Continued to the left as far as the point designated the 'left point' of the greater curvature, the colon forms a loop upwards before bending backwards at its splenic flexure. The middle of the highest part of this terminal loop upwards of the transverse colon (see fig. 3A, Part I.) practically corresponds to the left point of the greater curvature of the stomach. In most cases the mutual pressure of the two viscera, supported by the small intestines and general abdominal pressure below, and pressed upon by the diaphragm and liver above, determines where shall be the left point of the greater curvature. The precise situations of these two 'points' are—of the highest point of the splenic bend of the colon, 2.9 cm. above E.F., and 10 cm. from the middle line; of the left point of the greater curvature, 3.5 cm. above E.F., and 10.7 cm. from the middle line.

The upward bend of the transverse colon to the left is thus 4 inches from the middle line, and rather over 1 inch above E.F.

The part of *the anterior surface of the stomach* which is not covered by the liver or the diaphragm (fig. 3A), and which is more or less in contact with the anterior abdominal wall, may be roughly defined as a triangular area having for its base a line passing 1.5 cm. below E.F., beginning 2.5 cm. to the right of the middle line, and continued across to the left costal margin; the apex of the triangle being along the left costal margin, 3 cm. above E.F.

*Concerning the posterior relations* of the stomach, a general description is necessary before giving the averages.

The parts behind the stomach in the hardened specimen, or in a good fresh subject, present a well-marked and regular concavity for the reception of the cardiac portion of the stomach, which Birmingham (6) aptly described as the 'stomach-bed.'

When the stomach is removed the convexity of the central part of the diaphragm downwards, produced by the heart, is seen. Passing to the left, this convexity passes into the concavity which lodges the summit of the stomach, and which projects, as a rule, 1 cm. higher than the highest point of the spleen. The concavity of the diaphragm, continued either from above downwards or from the left inwards, passes into the hollow of the gastric surface of the spleen; this gastric surface of the spleen forming, with the diaphragm, the completion of the outer wall and a part of the floor of a deep concavity which projects backwards to a plane, up to 6 cm., posterior to the front of the aorta and the pancreas in the middle line. The floor of this concavity is completed, below the innermost part of the spleen, by a portion of the anterior surface of the left kidney at its upper part, the extent of this gastric surface of the left kidney being determined by the size of the spleen, and by the degree of displacement of the pancreas, as will be subsequently shown. Lying over the inner part of this portion of the kidney, and completing the floor of the stomach-bed at this part, and continuing it inwards to the side of the vertebræ, is a varying part of the left supra-renal capsule projecting above the upper border of the pancreas.

The extent of the gastric surface of the left supra-renal capsule is determined partly by the position of the convolutions of the splenic artery, which often quite overlap it, partly by

the size of the pancreas and the spleen, and partly by the position of the pancreas. When the pancreas is pushed upwards by the intestines below, or downwards by the stomach above, it sometimes carries the supra-renal body with it a certain extent. Moreover, when the upper portion of the spleen is enlarged, it spreads downwards over the gastric surface of the left supra-renal as well as over that of the adjoining kidney and shuts them out from relation with the stomach.

The concavity of the stomach-bed passes downwards from the hilum of the spleen, and from the gastric surfaces of the left kidney and supra-renal capsule, on to the gastric surface of the pancreas. The slope of the gastric surface of the pancreas is directed downwards and forwards, with varying degrees of obliquity, to the lower, or, more correctly, the anterior border of the gland. The degree of obliquity of the gastric surface of the pancreas is determined, with a pancreas of average size, by the pressure of the stomach above, and of the jejunum and intestines on the inferior surface of the pancreas below.

If the stomach is large, it tends to flatten the pancreas; and if it is large and lowly placed, it tends not only to flatten out the pancreas, but also to push it downwards over the face of the left kidney, with perhaps the left supra-renal capsule. On the other hand, if the intestines are distended, particularly the jejunum, they tend to push the pancreas bodily upwards over the left kidney, so that the gastric surface of the kidney may become obliterated, and, moreover, at the same time the anterior border of the pancreas is pressed upwards so that the inferior surface looks first directly downwards, then downwards and forwards; the slope of the gastric surface thus running increasingly forwards, the pancreas forming more and more a projecting ledge on which the stomach rests, not only posteriorly, but inferiorly. Furthermore, in this change the pancreas seems to be so moulded that there is an actual increase in the extent of its inferior surface, and a decrease in the extent of its gastric surface. The projecting anterior border of the pancreas presents between the jejunum below and stomach above. Fig. 1, Plate LIV., shows the different positions of the parts in the stomach-bed in the low and high positions of the stomach from two consecutive cases.



Permanent hardened preparations from cases 1 and 2 of this series illustrate very well these different points in connection with the stomach-bed.

If the stomach should project, as it usually does, below the anterior border of the pancreas, it is supported behind by the layers of the transverse meso-colon as they pass forwards.

The transverse meso-colon completes the stomach-bed behind and supports it below—the meso-colon being supported in its turn by the convolutions of the small intestine, as well as, perhaps, being held up, or even dragged up, by a distended transverse colon,—which, if convoluted, the small intestines being at the same time distended, may find room for itself by passing upwards over the front of the stomach. The stomach-bed at the left and below is completed by the splenic flexure of the colon, where the colon passes backwards across the basal surface of the spleen.

Finally, traced internally, the inner wall of the stomach-bed is formed by the diaphragm fibres passing downwards to the left crus across the sides of the vertebræ, and supporting in part the left supra-renal body. Internal to the supra-renal, as a rule, a portion of the left semilunar ganglion presents.

The pancreas traced internally passes into a convexity over the front of the vertebral column and aorta, and often presents a well-marked ridge as figured by His. This ridge on the pancreas was not usually found to be median in position. It was, when present, mostly situated to the left of the middle line, having a direction downwards and inwards, corresponding to a groove often present on this part of the stomach.

The pancreas in the average of the cases projected .5 cm. above the lesser curvature of the stomach in the middle line, and the stomach passed to the right as far as the pylorus, lying on the pancreas, the gland being moulded for its reception.

The anterior border of the pancreas, traced inwards from over the left kidney, becomes in the middle line, where it overhangs the emergence of the mesenteric vessels, the *lower* border of the body of the pancreas. It represents at this place the conjoined anterior and posterior borders, the inferior surface having ceased. However, even in the middle line, this border will always be spoken of as the *anterior* border.

## AVERAGES.

After the foregoing detailed description of the stomach-bed, the following averages suffice for this section.

The upper border of the pancreas in the middle line reached 2·4 cm. above the level of E.F., ·5 cm. above the lesser curvature. The greater curvature in the middle line overhung by 1 cm. the commencing anterior border of the pancreas, which here was 1·5 cm. below E.F. The vertical depth of the pancreas in the middle line, from the upper to the anterior borders, was therefore 3·9 cm. In the left lateral line the greater curvature projected 1·55 cm. lower than the anterior border of the pancreas, which here was situated ·3 cm. above E.F.; the extent to which the stomach projects below the anterior border of the pancreas indicating the extent to which it is supported behind by the transverse meso-colon.

The pancreas extended 9·1 cm. to the left of the middle line, and on the same transverse plane as its extreme left point the extent of the greater curvature to the left was 9·5 cm.

The line E.F. passes across the upper part of the head of the pancreas, and represents at the left costal arch its anterior border.

The upper pole of the left kidney, at a distance of 6·16 cm. from the middle line—practically the lateral line—was situated 4·5 cm. above E.F. The upper border of the pancreas in the same vertical plane was 3·4 cm. above E.F., thus leaving an average possible gastric surface of the left kidney of practically 1 cm.

In the left lateral line the average depth, in the vertical plane of the gastric surface of the pancreas, was 3·1 cm., and the depth, antero-posteriorly, of its inferior surface was 2 cm.

Behind the pancreas the inner convexity of the upper segment of the left kidney was situated 3·8 cm. from the middle line. The extreme outer point of the kidney, at an average level of ·6 cm. below E.F., was 9·6 cm. from the middle line. The extreme outer point of the left kidney was therefore situated a little lower and a little more to the left than the extreme left of the pancreas.

The lower border of the left supra-renal capsule was situated 5 above E.F.; its upper point about 2 cm. above the upper border of the pancreas and 5.5 cm. above E.F., and its innermost point, usually also its lowest point, 2.4 cm. from the middle line.

The lowest point of the anterior border of the spleen was situated 1.4 cm. below E.F., 11.5 cm. from the middle line, or .75 cm. more to the left than the extreme left point of the greater curvature of the stomach.

In those cases in which there was no marked angle at the lower border of the spleen, but in which the anterior border sloped gradually into the basal surface, the 'lowest point' had to be selected arbitrarily. The lowest point of the whole spleen, usually at the back of the basal surface, was situated 2.5 cm. below E.F. The highest point of the spleen was 8.7 cm. above E.F., 1.1 cm. below the infra-sternal notch, and 5.8 from the middle line. The innermost point of the spleen was situated a little above the level of the left kidney, 3.6 cm. from the middle line.

### III. VARIATION IN THE SHAPE OF THE STOMACH.

The outline of the stomach, seen from the front, as obtained in this work, does not necessarily indicate what would be its shape if it were removed from the body and filled. The outlines (see Plates XLIII. and XLIV., Part I.) are no doubt determined very much by the pressure of surrounding viscera. But allowing for this, the cases do, perhaps, furnish some indications of certain natural varieties in shape.

*First variety.*—A type of stomach, usually not of large size, and characterised by a long cylindrical portion passing to the pylorus, is, perhaps, the commonest. Examples of this shape are seen in Nos. 1, 3, 6, 8, 18, 20, 25, 30, 31, 35, and 37, and to a less extent in Nos. 17, 24, 26, 27, 33, and 40—that is, in 42.5 per cent. of the total cases. Sometimes it was plain that the shape was produced, to a great extent, by the pressure of the transverse colon. For instance, the stomach in case 21 might seem deservedly to be included in this group, but reference to the complete plate of the case shows that the appearance is produced by the pressure of the adjoining colon. (The

figures of the colon will be published in a subsequent number of the *Journal*.)

In connection with this type of stomach, it will be seen that they represent amongst them all those in which the stomach was highly placed, except No. 12 in which the stomach was of a somewhat similar shape. The high position of these stomachs is most likely accounted for by the fact, that they contain amongst them all those cases in which a distended transverse colon passed highly upwards in front of the stomach,—viz., cases 1, 6, 8, 25, 31, 35, 37 and 40, with case 12; and in others of the group the colon was distended, though not in front of the stomach, as in cases 20 and 18; in which last case also the jejunum was distended. It is clear that a distended transverse colon was associated very commonly with this shape of the stomach, and, presumably, was to some extent responsible for it. I think, however, that it is open to question, seeing, for instance, that the stomach from case 1, which was removed from the body and filled with agar jelly, still retained its shape, whether this type of stomach, being mostly small, does not, if the colon becomes distended, as it were, invite the bowel to seek its additional room in the upper part of the abdominal cavity; so that a distended colon high in the abdomen may not alone be the cause, but, perhaps, to some extent, the consequence of a stomach this shape.

In case 27 the stomach and liver were pushed down by a large intra-thoracic growth.

Eight of the subjects with this type of stomach were emaciated, and had suffered from long-standing disease.

*Second variety.*—The stomachs Nos. 5, 12, 15, 19, 23, and 36, and to a less extent Nos. 4, 11, and 24, show evidence of a *constriction* somewhere in the cardiac portion, that would no doubt have been permanent—cases 23, 36, 15, and 5. being the best examples. The constriction, when present, tends to be about half-way along the left border of the greater curvature.

*Third variety.*—A third type of stomach, almost evenly cylindrical and usually capacious, is represented by Nos. 2, 7, 10, 22, 38, and 39, also by No. 14—the kink in which was produced by the pin. Nos. 21, 24, and 34 probably represent intermediate states between this type and the elongated con-

stricted stomach of Nos. 15 and 36. Several of these were, apparently, chronically distended.

These cases did not present much in common. Four were emaciated, and had suffered, three from phthisis, and the other from tubercular salpingitis. The other cases presented various diseases. Three of the subjects are described as fat.

*Fourth variety.*—Some of the other stomachs which were distended presented a more quadrilateral shape, of which No. 16, which was pushed over to the left by a large liver, is the best example. Nos. 9, 28, 29, and 32 are of a similar shape; but the straight lower border in cases 28 and 29 was distinctly produced by a distended straight transverse colon.

Cases 13, 31, and others, show also quadrilateral features.

#### IV. VARIATIONS IN THE POSITION OF THE STOMACH.

**THE CARDIAC ORIFICE.**—The outlines on Plates XLIII. and XLIV. (Part I.) show these variations much better than a mere statement of numbers can. The general position of the centre of the cardiac orifice, 2.1 cm. below the infra-sternal notch and 1 cm. from the middle line, agrees very well with that given in most text-books. There was, however, in this part of the stomach, an excursion of its central point about the infra-sternal notch of 7 cm.; from 6 cm. below in case 7, to 1 cm. above in cases 4 and 34.

*High Positions.*—In three instances, Nos. 4, 12, and 34, the centre of the cardiac orifice was above the infra-sternal notch, the maximum being 1 cm. In the first of these, a patient with phthisis, the stomach was large and full. There is no record of distension of the rest of the intestine. The transverse colon was low and tortuous. In the second instance, a case of pneumonia, the jejunum and cæcum were very distended, the transverse colon was full, and the splenic flexure of the colon reached high up to the left of the stomach into the vault of the diaphragm. In the third case, with pulmonary phthisis and some tubercular peritonitis, the small intestines were very distended, but the colon was in its normal position. In this case (see Plate LII.) the liver was very large, and extended to the left across the stomach, overlapping the spleen.

*Low Positions.*—There were six cases in which the centre of the cardiac orifice was 4 cm. or more (up to 6 cm.) below the infra-sternal notch (Nos. 7, 15, 18, 27, 30, and 35). The first was a case of right pneumothorax, with the liver and stomach pushed down. The second case presented a large intra-thoracic tumour, with a similar displacement of the stomach and liver. In the third, although the upper border of the stomach was lower than the average, the lower border was higher than usual, and was supported by distended intestines above a low transverse colon. There is nothing recorded from the thorax to account for the low cardiac opening; the costal arch was narrow. In the fourth case there was a large secondary sarcomatous growth in the thorax, especially in the left side; the transverse colon was distended and low. In the fifth case there was no special factor recorded; the small intestines were distended, but the transverse colon was low down, running across the pelvic cavity. In the last case, one of advanced phthisis, the lower border of the stomach, again, was higher than usual, but the cause of displacement of the upper border downwards was quite obvious, for a huge transverse colon had passed up in front of the stomach, pushing the liver over to the right, and insinuating itself between the stomach below and diaphragm above. It is unfortunate that a record of the condition of the heart was not made in all these cases, especially in case 18.

CONCLUSIONS.—The chest conditions, as would be anticipated, seem the most important in producing *downward displacements of the cardiac part* of the stomach, even against considerable intestinal distension below.

*Upward displacement* is usually associated with distension of the intestines, and often with a transverse colon passing upwards in front of the stomach. But, on the other hand, it is clear that distension of the intestines, even when there is absence of any obvious thoracic opposition, is not always associated with a raised cardiac orifice, as cases 18 and 35 show. The distension of the transverse colon, in fact, in the last case, as already explained, was the actual cause of the downward displacement of the cardiac orifice.

*The relative levels* of the cardiac and pyloric orifices are

shown on curve A, Plate LIII. Although there is a general correspondence in the levels, cases 11, 14, and 40, in addition to those already quoted, show that the stomach may be full and have a normally situated, or even raised, pylorus, and that yet there may be a low cardiac opening; the mutual abdominal and thoracic pressures causing the transverse diameter of the stomach to be much the longer.

**THE PYLORUS.**—If the outlines on Plates XLIII. and XLIV. (Part I.) or curve B on Plate LIII. be consulted, it will be seen that in 24 cases, or 60 per cent. of the whole series, the line E.F. passed through some part or other of the pylorus, or was within half a centimetre of one of its margins; and that in 29 cases, or 72·5 per cent., it passed either through the pylorus, or within a centimetre and a half of its margins.

1. *Vertical Displacements.*—There were 29 cases in which the upper border of the pylorus was in the plane of, or above the level of E.F. In 24 of them the distance did not exceed 3 cm., and in the remaining 5 cases (Nos. 25, 40, 5, 37, and 31) the greatest height above E.F. was 6·5 cm., in case 31.

There were 11 cases in which the upper border of the pylorus was *below* the level of E.F., 5 of them being at or less than 2 cm. below; the remaining 6 cases (Nos. 32, 34, 7, 36, 15, and 2) being more than 2 cm., up to 6·5 cm. below, in case 2.

(a.) *High Position.*—The colon was distended in each of the five cases in which the pylorus was highly situated (those in which the upper border was more than 3 cm. above E.F.), and in four of them (Nos. 25, 40, 37, and 31) passed upwards to a variable height in front of the stomach. In the other case, No. 5, a distended jejunum pressed up the stomach. In these cases the liver was pressed upwards and to the right, and was noted to be small in cases 5, 31, and 37. (See the outlines on Plate LII., and the curves B, C, and D of Plate LIII.)

(b.) *Low Position.*—Five of the 6 cases in which the pylorus was situated low down (the upper border more than 2 cm. below E.F.) were associated with a large or displaced liver—cases 34 and 36 with large lardaceous livers, case 15 with an immense liver pushed down by a large growth filling the right side of the chest, case 7 with a liver displaced by a right pneumothorax,



and case 2 with a large and somewhat low nutmeg liver. In all of these 5 cases also the stomach was distended, and was vertically elongated. In case 24, although not coming under this arbitrarily-defined group, the pylorus was displaced downwards and to the left by a large lardaceous liver, the stomach being of the elongated variety. The remaining case in which the pylorus was more than 2 cm. below E.F. (3 cm.) was No. 32. In this case the liver was small and pushed over to the right, the pylorus following it on its under surface, and a distended stomach lay horizontally across the abdomen, nearly bisected by E.F. In this case, as well as in all the others presenting a low pylorus, there was a low, prolapsed transverse colon (case 34 being the least marked). In Nos. 7, 32, and 36 there was a considerable interval between the upper border of the prolapsed transverse colon and the greater curvature of the stomach, in which the stomach was supported behind the meso-colon by the small intestines.

*Downward Displacement of the Stomach.*—Now, a stomach may be full, in fact distended, without coming appreciably much lower in the abdominal cavity, as outlines 9, 10, 16, 23, 28, and 29 on Plates XLIII. and XLIV. clearly show. But it is the stomach elongated vertically (however that elongation may have been produced) which is found low in the abdominal cavity, and whose position is usually associated with a liver enlarged or displaced downwards and a prolapsed or low transverse colon.

Although not quite *apropos* of the position of the pylorus, it will be convenient to take here the other cases in which the stomach reached low down in the abdominal cavity. In case 38, in which all the parts were loaded with fat, and the parts of the gastrointestinal canal were very capacious, with some most noteworthy features, the stomach was very flabby, and of immense size, and came 10 cm. below E.F. in the middle line. The *liver* was not enlarged, and occupied its normal level, and the *pylorus* was at its usual height. In this case the transverse colon ran along the lower border of the stomach to the left lateral line, where it passed upwards beneath the stomach to the splenic flexure, which was situated 1 cm. above the level of E.F. In case 39, in which there was acute general peritonitis from the rupture



of a left tubal abscess, with a large quantity of fluid in the abdominal cavity, the stomach was 8 cm. below E.F. in the left lateral line; there was a large liver extending low down, at the right, and with a thin flap overlying the stomach below E.F. to the left of the middle line, and a distended transverse colon passing across below the greater curvature of the stomach. The upper border of the pylorus in this case was situated *in the plane of E.F.*, .75 cm. to the right of the middle line. In case 30, in which the greater curvature in the middle line was 4 cm. below E.F., there was a prolapsed transverse colon running across the pelvic cavity, and the liver was a little lower than usual, the upper border of the pylorus being 1.5 cm. below E.F., and 1.25 cm. to the right of the middle line. Finally, in case 22, there was a large liver pushed down and over to the left by very firm pneumonic consolidation of the right lung, and the stomach was lying vertically; the upper border of the pylorus was situated 3.75 cm. to the left of the middle line in the plane of E.F. The transverse colon was low and tortuous.

#### CONCLUSIONS.

1, i. In considering the foregoing cases, it appears that a *highly-placed stomach* is usually associated with a liver placed well up beneath the ribs and often small, and with a highly-placed transverse colon, which in most cases was also distended. But as regards the colon, it appears that it may come upwards *in front* of the stomach without appreciably elevating the stomach itself; merely pressing it backwards into the stomach-bed.

ii. As regards a *low position* of the stomach, referring generally to the greater curvature, it appears to be specially associated with the liver extending low down in the abdomen, and perhaps enlarged, and with a prolapsed colon. On the other hand, however, by an increase of the length of the peritoneal fold attaching the colon to the lower border of the stomach, the transverse colon may sink away from the greater curvature of the stomach, leaving the stomach supported, *at its usual level*, by the intestines behind a long transverse meso-colon.

As regards the alterations in level of the *pylorus*, in particular, it is clear that the liver is the chief determining factor;

that when the liver extends low down in the abdominal cavity, the pylorus is generally lowly placed, and *vice versa*; allowing for the fact that the part of the liver overhanging the stomach varies considerably in thickness, it appears, as case 38 shows very well, that *mere distension* of the stomach, apart from a low position of the liver, does not suffice to produce material downward displacement of the pylorus. This matter, however, will be more fully set forth in the course of the following section.

2. *Lateral Displacements of the Pylorus*.—Following the suggestion contained in the preceding paragraph, it is found that with regard to the position of the pylorus to the right or left of the middle line, a matter as important as, if not more important than the degree of the distension of the stomach at any particular time, is the position of the liver, and, more particularly, the shape of its under surface. By means of the strong right part of the lesser omentum, and the structures contained within it, connecting the pylorus and the first part of the duodenum to the under surface of the liver, the pylorus is firmly held up to the transverse fissure of the liver, and its position and obliquity by this means considerably determined.

Taking first a summary of the various positions of the pylorus:—In 34 cases it was on the middle line or to the right of it; and in 6 cases to the left.

Analysing the first group of 34 cases:—In 14 instances (in three of which some part of the pyloric border touched the middle line) the pylorus was up to or less than 2 cm. to the right of the middle line. In a further 14 cases it was more than 2 cm., up to or less than 4 cm., to the right of the middle line. Beyond this distance to the right there were 6 cases; 4 of them up to, or less than, 4·5 cm. from the middle line; and two cases, Nos. 35 and 4, were 5 cm. and 6 cm. respectively from the middle line. In both these the greater curvature of the stomach was at a higher level than usual.

Of the 6 cases in which the pylorus was situated to the *left* of the middle line, 4 were up to or less than 2 cm. away, the remaining two (Nos. 22 and 24) were 3·5 cm. from the middle line.

(These measurements in all cases relate to the upper border of the pylorus.)

The figures yield the result that *in 45 per cent. of the cases the upper border of the pylorus was not more than 2 cm. from the middle line to one side or the other*: that in 22·5 per cent. of the total cases the pylorus was in the middle line or to the left of it; and that in 15 per cent. only of the cases was it situated more than 4 cm. to the right of the middle line.

The direction of the pylorus in 24 cases, or in 60 per cent. of the whole series, was practically vertical; in 10 cases it was oblique, and in the remaining 6 cases it was practically transverse. (Cases 2, 21, 24, 32, 34, and 38.)

(a) *Displacement of the Pylorus to the left.*—As to the cause of these lateral displacements of the pylorus: In those in which the pylorus was situated *on the middle line or to the left thereof*, the liver was in all cases, except the first, very manifestly the cause of the displacement. In the first case (No. 3), in which the pylorus was 1 cm. to the left of the middle line, the patient had died of prolonged sepsis, the liver had a massive omental tuberosity fitting into the lesser curvature, but it did not extend to the left of the middle line in the plane of the upper border of the pylorus; the stomach was small, and, like all the other parts of the gastro-intestinal canal, empty. In all the other cases, in Nos. 13, 15, 16, 22, and 24, in which the pylorus was to the left of the middle line, and in Nos. 7, 19, and 39, in which it was on the middle line, the liver extended low down and far over to the left at a low level, being either enlarged itself through disease, or displaced downwards by thoracic pressure. An attempt is made on the curve on fig. 2, Plate LIV., by depicting the relation of the upper border of the pylorus and of the lower border of the liver in the same horizontal plane to the middle line, to represent the conditions. The curve shows that these cases were accompanied by a considerable extension of the liver over to the left of the middle line.

The curve, however, is to some extent misleading. For instance, in case 2, in which the lower border of the liver is represented far to the right of the pylorus, the Plates XLIII. and LII., on comparison, show that the liver presented a nearly straight lower border 5 cm. above the level of the upper border of the pylorus, and that, although the lower border of

the liver, in the same plane as the pylorus, was so far to the right thereof, yet, at only 1 cm. higher level, the lower border of the liver crossed the middle line. A similar condition existed in case 3, in which a portion of the extreme right of the liver came into the curve, whilst at a level of only .25 cm. above the pylorus, the lower border of the liver crossed the middle line; and in case 37, in which an enormously distended colon pushed up the liver and stomach; also, in case 32, in which the liver was pushed up higher than usual by a very large dilated stomach. Case No. 32 exhibits the condition Prof. Symington (10) figures as the state of the distended stomach; but, as will be pointed out, these cases do not seem to warrant one in describing it as the normal condition of the distended organ.

If we consider the instances on the curve, and on the Plates in which the lower border of the liver extended far over to the *left* of the middle line in the same plane as the upper border of the pylorus, but in which the pylorus was not displaced to the left, it will be seen that in 2 cases, Nos. 6 and 26, the liver was as high or higher than usual, and that the pylorus had been pushed over *to the right* beneath the liver; in the first case by a high distended colon, and in the second case by a full stomach. In case 27 the liver was displaced downwards by a growth in the thorax, chiefly on the left side, and the left part of the liver being tilted down depressed the lesser curvature some distance from the pylorus. In case 33 the liver was fatty, but did not descend much lower than usual, and pressed by its omental tuberosity, as in the last case, chiefly on the lesser curvature beyond the pylorus. The remaining instance, No. 38, is very instructive, for it shows how little even an enormously dilated stomach is able to drag the pylorus downwards whilst the liver maintains its normal level.

*Summing up the displacements of the pylorus to the left*, the cases show clearly that the liver is the chief determining agent, and it seems that we could from these cases go so far even as to say that, *when the liver is enlarged and spreads downwards across the abdomen at a low level*, we may expect the pylorus to be pushed to the middle line or to the left thereof.

Although a consideration of these cases does not lead us to the conclusion that a pylorus situated to the left of its normal

situation is particularly associated with an empty condition of the stomach, if we look at those cases in which the pylorus is situated more than 1 cm. *to the right* of its average position, we find that they are particularly associated with a well filled or distended condition of the stomach.

(b) *Displacements of the Pylorus to the right.*—Symington (10) pointed out how the left overhanging part of the liver is tilted upwards and to the right on its long left lateral ligament by the filling stomach. If this ligament be long and membranous—even if the part of the liver overhanging the stomach is somewhat massive—the distended stomach can the more readily tilt the liver upwards and to the right, and insinuate itself further to the right underneath the liver. The strong attachment, already spoken of, of the pylorus to the under surface of the liver, would not resist a considerable movement of the pylorus to the right, as it does to the left, because of the obliquity of the attaching part of the lesser omentum.

If the liver be looked at from the front, a fair guide to the degree of lateral movement it has undergone may be obtained by noticing the situation and direction of the attachment of the falciform ligament on its anterior surface. On the diagrams of the liver on Plate LII., and on the composite figures of each case, with the exception of a few of the early cases in which, unfortunately, the point was omitted, the attachment of the falciform ligament to the liver is indicated by interrupted lines.

Those cases in which the pylorus was displaced to the right are so uniform, that, with the various illustrations, and the points already mentioned, it will be sufficient to represent them here in tabular form; and in reading the table, it will render the matter clearer if Plates XLIII., XLIV. and LII. be compared at the same time.

In the table only those cases are represented in which the pylorus extended 3·5 cm. or more to the right of the middle line.

| CASE. | Distance to right of middle line of the upper border of the Pylorus. | REMARKS.  |
|-------|--|---|
| 2     | 3·5 cm.  | Stomach distended and low. Liver <sup>1</sup> a little tilted, low, and somewhat enlarged. Colon, no special feature.   |
| 14    | "  | Stomach full. Liver tilted. Colon very distended, pressing up the stomach.  |
| 21    | "  | All points the same as No. 14.  |
| 26    | "  | Stomach full, thrown into folds. Liver not much tilted. Transverse colon normal.  |
| 27    | "  | Stomach moderately filled. Stomach and liver both pushed down by intra-thoracic growth. Liver not tilted. Colon very tortuous and distended.  |
| 11    | 4 cm.  | Stomach full. Liver tilted.   |
| 28    | "  | Stomach distended. Liver tilted and much pushed over to the right. Colon distended.   |
| 29    | "  | Ditto in all respects.  |
| 5     | 4·5 cm.  | Stomach full. Liver and stomach pushed up and to the right by distended colon and intestines.   |
| 10    | "  | Stomach very distended. Liver pushed almost entirely to the right of the middle line.   |
| 32    | "  | Stomach very distended. Liver much tilted. Transverse colon prolapsed.  |
| 28    | "  | Stomach very distended. Liver tilted.   |
| 35    | 5 cm.  | Stomach partly filled, thrown into folds. Liver and stomach both pushed upwards and to the right by an enormously distended colon. Liver almost entirely to the right of the middle line. |
| 4     | 6 cm.  | Stomach distended. Liver large, not much tilted to the right. Colon low and tortuous.   |

### MOVEMENTS OF STOMACH.

In this place it will be convenient to summarise the impressions received concerning the movements of the stomach.

Although there were so many cases in which the stomach was well filled and distended, there was only one example (case 32) of the condition figured by Symington (10) in which the pylorus, in the distended stomach, was situated behind a portion of the stomach that had extended across to the right in front of the pylorus.

<sup>1</sup> The tilting of the liver is of the left lobe to the right and upwards.

I cannot but think that if this were the usual condition in distension, more examples would have been met with. In cases 34 and 38, however, a portion of the greater curvature passed well to the right beyond the pylorus, though at a lower level.

In those cases in which the pylorus ran transversely, or nearly so (Nos. 21, 24, 32, 34, and 38), the condition was clearly due to its being firmly held in this position to the transverse fissure of the liver. We have seen that a pylorus well over to the right is specially associated with a full stomach; but those cases, as I have indicated at various times, and as the figures show, by no means include all those in which the stomach was full; and, moreover, except in one case, No. 3, the pylorus did not tend to be situated markedly to the left of its average situation when the stomach was empty. I do not think that these cases warrant us in concluding that during filling of the stomach the pylorus moves more than 2 cm. to the right, if at all. *Movements of the pylorus to the left* have already been considered.

*Filling of the Stomach.*—As regards what would seem to take place during the process of filling of the stomach:—Apparently the stomach-bed behind is first occupied; then the greater curvature in front, to the left of and below the liver, comes to the abdominal wall, at the same time tilting upwards and to the right the left lobe of the liver, and directing the lesser curvature somewhat to the right and backwards; then, if necessary, the stomach extends somewhat to the right, downwards and forwards, pressing down before it the projecting anterior border of the pancreas and the transverse mesocolon.

#### SUMMARIES.

After the previous detailed statement of the variations in the position of the stomach, particularly of its two orifices, a summary of the chief variations of the other 'points' will suffice.

*The extreme left of the lesser curvature from the middle line.*—The average was 3.8 cm. There were 13 cases in which the distance was 5 cm. or more, up to 7 cm. in case 13. There were

12 cases in which the distance was 2·5 cm. or less, down to ·5 cm. in case 35. The point nearest to the plane of E.F., at which the lesser curvature attained its extreme left, averaged 4·5 cm. above E.F. There were 16 cases in which it was 6 cm. or more, up to 9 cm. (in 2 cases) above. There was one case in which it was below E.F. (4 cm. in case 7); and 4 cases in which it corresponded with E.F.

*The lesser curvature in the middle line as to E.F.* averaged 1·9 cm. above. There were 19 cases in which it corresponded with E.F., or was up to or as much as 3 cm. above. There were 14 cases in which it was more than 3 cm. above E.F., up to 7 cm.; in 7 of them being 5 cm. or less above. In 3 cases it was up to 1·5 cm. below E.F., and in 4 cases was more than this distance below, down to 6·5 cm. in case 2.

*The height of the summit of the stomach above E.F.* averaged 9·6 cm. In 11 cases it was 11 cm. or more above, up to 14·5 cm. in case 10. In 10 cases it was 8 cm. or less above, down to 6·5 cm. in cases 2 and 7.

*The summit of the stomach as to the infrasternal notch* averaged ·13 cm. below. In 24 cases it was either at the same level or below; in 19 of these being not more than 1·5 cm. below. There were only 3 cases in which it was more than 3·5 cm. below. In the lowest instance, case 37, it was 4·5 cm. below.

There were 16 cases in which the summit of the stomach was above the level of the infrasternal notch; in 9 of them not being more than 1·5 cm. above. The highest was 4·5 cm. above in case 10.

*The point along the plane of the summit of the stomach which was nearest the middle line* averaged 5·1 cm. away. In 36 cases the variation was not more than 1 cm. either way from the average. One case, No. 24, was 3 cm. Three cases were beyond 6 cm., the extreme being 8·5 cm. in case 1. (In the light of later work I cannot but regard some of the measurements recorded in case 1 as of doubtful accuracy.)

*The extreme left of the greater curvature from the middle line* averaged 10·7 cm. There were 20 cases more than the average, and 20 cases less. Of these, 16 cases, each way, did not approach the middle line nearer than 9 cm., or extend more than 12 cm. away from it.



The distance, therefore, in 80 per cent. of the cases was between 9 and 12 cm., inclusive, from the middle line. Cases 9 and 16 presented the extreme distance to the left, 13·5 cm.; and case 2 the near limit of 8 cm.

*The distance of the point, in a vertical plane through the extreme left of the greater curvature, which was nearest to E.F. averaged 3·5 cm. above that line. In 21 cases it ranged from 2 cm. above to 4 cm. above, inclusive; in 5 cases from 4 cm. to 6 cm. above, inclusive; 4 cases were at 7 cm. above, and 2 beyond this; the extreme being 10 cm. in case 12. In the remaining 8 cases, 7 were on the level of E.F., and 1, case 24, 4 cm. below it.*

*The greater curvature in the left lateral line as to E.F. averaged 1·2 cm. below. In 20 cases the distance above or below E.F. did not exceed 2 cm. either way. More than 2 cm., up to and including 4 cm., there were 5 additional cases each way. There were 2 cases more than 4 cm. above E.F., the extreme being 5·5 cm. in case 40.*

There were 8 cases more than 4 cm. below E.F., and 4 of them were more than 8 cm. up to 11·5 cm. below, in case 35. *If these four lowest cases be excluded, the level of the greater curvature in the left lateral line would be E.F. exactly.*

*The greater curvature in the middle line as to E.F. averaged 2·5 cm. below. From the level of E.F., up to and including 4 cm. below, there were 25 cases—62·5 per cent. There were 4 cases up to or as much as 2 cm. above E.F.; and 3 cases higher than this, the extreme being 4 cm. above in case 31.*

The remaining 8 cases were from 6 cm. below E.F. to 13 cm. below in case 2. If these 8 cases of low stomachs be excluded, the level of the greater curvature in the middle line in the remaining 80 per cent. of the cases would average 1·2 cm. below E.F., instead of 2·5 cm.

## DESCRIPTION OF PLATES.

## PLATE LII.

The lines from the whole series of cases shown on a scale representing centimetres in relation to the costal arch, the middle line and E.F. (a line drawn transversely across the body through a point midway between the upper border of the pubes and the suprasternal notch).

## PLATE LIII.

Curves illustrating various points in connection with the relation of the stomach to the liver and the transverse colon, and of the positions of the orifices of the stomach.

## PLATE LIV.

Fig. 1. Showing the position of the parts behind the stomach when it is lowly placed—case 36—and when it is highly placed—case 37.

Fig. 2. Curves showing the relations of the upper border of the pylorus and the lower border of the liver in the same horizontal plane to the middle line.

- <sup>1</sup> Distance of the *cardiac orifice* above or below the *infra-sternal*  
" " " above E.F.,  
" " " from the *middle line*,

#### The Lesser Curvature.

- <sup>2</sup> Distance of the *extreme left* from the *middle line* ('left point')  
<sup>2</sup> " of the *above point* above or below E.F.,  
<sup>3</sup> " in the *middle line* above or below E.F.,  
" of the *upper border* of the *pylorus* above or below E.F.  
<sup>3</sup> " " " " from the *middle line*

#### The Greater Curvature.

- Distance of the *summit* of the *stomach* above or below E.F.,  
" " " " the *infra-sternal*  
" " " " from the *middle line*,  
<sup>2</sup> " of the *greater curvature* to the *left* of the *middle line*  
<sup>2</sup> " of the *above point* ↑ above or below E.F.,  
" in the *left lateral line* above or below E.F.,  
" as it *passes beneath* the *costal arch* above or below E.F.  
<sup>3</sup> " in the *middle line* above or below E.F.,  
<sup>4</sup> " of the *right extremity* of the *stomach* from the *middle*  
<sup>4</sup> " of the *above point* above or below E.F.,

#### The Liver.

- Distance of the *lower border* of the *liver* above or below the *upper border* of the *pylorus* in the *same vertical plane*,  
\* Distance of the *lower border* of the *liver* above or below *lesser curvature* in the *middle line*,  
<sup>2</sup> Distance of the *liver* to the *left* in the *same plane* as the "*lesser curvature*,"—more, *m*, less, —,

#### The Pancreas.

- Distance of the *upper border* of the *pancreas* in the *middle line* above or below E.F.,  
Distance of the *upper border* of the *pancreas* in the *middle line* above or below the *lesser curvature*,  
Distance of the *anterior border* of the *pancreas* in the *middle line* above or below E.F.,  
Distance of the *anterior border* of the *pancreas* in the *middle line* above or below the *greater curvature*,  
Distance of the *anterior border* of the *pancreas* in the *left lateral line* above or below E.F.,  
Distance of the *anterior border* of the *pancreas* in the *left lateral line* above or below the *greater curvature*,  
Extent of the *pancreas* to the *left* of the *middle line*,  
" *greater curvature* to the *left* of the *middle line* in the *middle line*

<sup>1</sup> The central  
<sup>2</sup> The extreme  
<sup>3</sup> In those cases  
<sup>4</sup> In most cases  
\* In cases 3,  
Note.—Average



DESCRIPTION OF A SPECIMEN IN WHICH THERE IS  
A RUDIMENTARY FIRST RIB ALONG WITH  
THIRTEEN PAIRS OF RIBS AND TWENTY-FIVE  
PRE-SACRAL VERTEBRÆ. By ALEX. LOW, M.B.,  
*Senior Assistant in the Anatomical Department, Aberdeen  
University.*

THE specimen is preserved in the Anatomical Museum, and was obtained in the summer session 1899, in the course of practical work in the department. It belonged to a male subject who had died from malignant disease of the stomach.

There are thirteen ribs on either side, and of these eight pairs join the sternum.

The *first left rib* is rudimentary, and presents the following appearances:—Its *head* articulates with the body of the *eighth* vertebra, and also slightly with the lower margin of the body of the *seventh*; the *neck* is well developed, but rather more flattened than that of the first rib of the right side; the *tuberosity* articulates with the transverse process of the eighth vertebra, and from the head to the tuberosity measures 30 mm. From the tuberosity the rib bends forwards, almost at a right angle, and 17 mm. in front of tuberosity there is a false joint, from this the bony part of the rib is continued for a distance of 39 mm., where it ends in rather a blunt point, covered with a tip of cartilage, which is connected by a strong fibrous band 18 mm. in length, to the first costal cartilage. This cartilage measures 26 mm. by about 8 mm. in depth. At its inner extremity, its lower border is fused with the upper border of the second costal cartilage for a distance of 10 mm.

The first rib on the *right* side also articulates with the bodies of the seventh and eight vertebræ, but otherwise presents all the characters of a normal well developed first rib.

The *second* pair of ribs are normal in form and direction, and articulate by their heads with the bodies of the first and second thoracic vertebræ, while their costal cartilages join the manubrium—that of *right* side at a point near the middle of the border

of the manubrium, that of *left* side joining the manubrium at a higher level.

The costal cartilages of the *third* pair of ribs join the sternum at the junction of the manubrium with the gladiolus.

Relations of the soft parts on the *left* side. Both *intercostal*

FIG. 1.

muscles in the first space were well developed. The *scalenus anticus* arose from the anterior transverse processes of the fourth, fifth, and sixth vertebræ, but mostly from the sixth transverse

process, and then passed between the vein and the artery to be inserted into the first rib, a little behind the point where it becomes fibrous. The *subclavius* muscle arose from the outer end of the first cartilage. The *scalenus medius* and *posticus* were attached to the upper surface of the first rib, just in front of its tuberosity, and also both to the second rib near its angle. The *subclavian* artery passed over the first rib, lying on a slightly smooth surface outside the attachment of the *scalenus anticus*. The *vertebral* artery passed through the transverse process of the sixth vertebra. The *posterior scapular* artery came off the subclavian at the outer border of the *scalenus anticus*. The *deep cervical* artery passed between the anterior divisions of the eighth and ninth spinal nerves and under the transverse process of the seventh vertebra. The greater part of the ninth nerve passed up over the neck of the first rib to join a division of the eighth, helping to form the brachial plexus, which was normal.

It is of interest to note that in both upper extremities there was a third head to the *biceps*.

The *twelfth* pair of ribs articulate with the upper border and pedicles of the nineteenth vertebra, and slightly with the disc above—they have no tubercles. Both are sloped well downwards and forwards, and the free extremity of each is tipped with cartilage. The *right* measures in length 135 mm., and in depth about 10 mm.; the *left* is of exactly the same dimensions.

The *thirteenth* rib on the right side is 41 mm. long and 5 mm. in depth. Its *head* articulates with the body and partly with the pedicle of the twentieth vertebra; its free end is blunt and has no cartilaginous tip. The *left* thirteenth rib is 69 mm. long and 7 mm. broad, and has a thick rounded head, articulating with the body and pedicle of the twentieth vertebra; its tip is pointed and covered with cartilage.

The *vertebral column* is peculiar in that there are twenty-five pre-sacral vertebræ. In the cervical region the foramen in the left transverse process of the fourth vertebra and also the foramina in both transverse processes of the sixth are divided into two compartments—a larger antero-internal and a smaller postero-external.

The *seventh vertebra* has all the characters of an ordinary last cervical vertebra. Its *spine* is long, and ends in a tubercle; its

*transverse* processes show hardly any indication of an anterior tubercle; there is no projection downward of the anterior margin of its body, but there is a pair of small half *costal facets* on its lower border.

The *eighth* vertebra is exactly like a normal first thoracic, only

FIG. 2.

there is a pair of costal half facets on the upper border of its body as well as corresponding half facets on its lower border.

The *nineteenth* vertebra carries the twelfth pair of ribs which articulate with the upper margin of its body and pedicle, and



very slightly with the lower border of the eighteenth vertebra, otherwise it has the characters of a normal last thoracic vertebra.

The *twentieth* vertebra carries the thirteenth pair of ribs which articulate near the upper margin of its body and pedicle on either side. Its *spine* slopes downwards rather more than that of a normal first lumbar vertebra; its *transverse* processes have more the character of those of a last thoracic vertebra, their superior tubercles being directed upwards and inwards; its superior *articular processes* are 35 mm. apart, while the inferior are 28 mm. apart.

The *twenty-fourth* vertebra presents the appearances of a normal last lumbar: its transverse processes are triangular and point upwards; its upper articular processes are 44 mm. apart, the lower 54 apart.

The *twenty-fifth* vertebra has also the characters of a normal last lumbar vertebra, but its transverse process on the right side is much thicker, while the lower border of the left transverse process is prolonged downwards, and is united with an uprising from the wing of the sacrum. Its upper articular processes are 55 mm. apart, the lower 54 mm.

The *sacrum* measures 93 mm. from above down, and 108 mm. from side to side, and is made up of five pieces, the transverse portion of the last being imperfect on the right, so that there are only three sacral foramina on that side.

The *coccyx* consists of three pieces—the first piece has no cornua and no transverse processes, so that it is like a normal second coccygeal vertebra. The last two pieces are mere rounded nodules closely fused. The last piece of sacrum is evidently formed by the first coccygeal vertebra having become ossified on to it. Its cornua are also united to those of sacrum—on the left side the line of junction is cartilaginous, on this side also its transverse process is prolonged upwards, and is ossified on to the inferior lateral angle of the sacrum.

The *sternum* is joined by eight pairs of rib cartilages, the eighth rib on each side joining at the angle between gladiolus and ensiform. The manubrium measures 59 mm. long and 56 mm. at its broadest, but it narrows below so as to be only 30 mm. broad where it joins gladiolus—each lateral border of manubrium has two complete facets for rib cartilages, and one



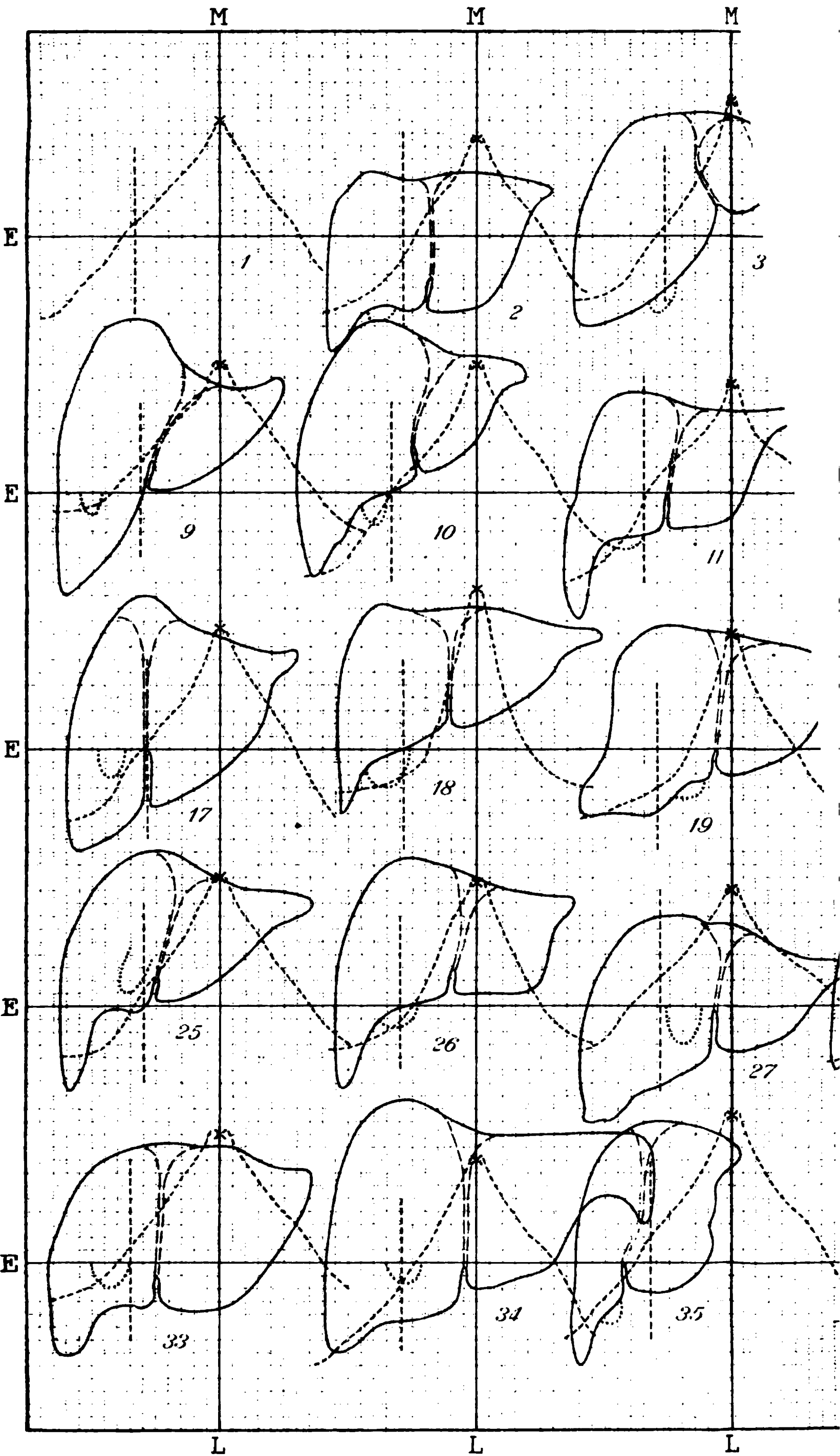
*Remarks.*—The chief feature in this specimen is the combination of abnormalities it presents ; for although any one of these abnormalities is not uncommon, it must be rare to have so many in a single specimen. Lane describes a somewhat similar specimen in the *Jour. of Anat. and Phys.*, xix. p. 266, 1881. In his case the rudimentary rib was associated with a like condition of the sternum, and also, as in the present case, there was a third head to the biceps in both arms. Lane regarded his specimen as an example of a supernumerary cervical vertebra bearing ribs. In the present instance there seems no doubt but that the extra vertebra is the first sacral, the forward shifting of the pelvis having been arrested at the twenty-sixth vertebra, a condition which is frequently associated with a thirteenth rib. Wiedersheim states that the thirteenth rib, which always appears in the embryo, begins to degenerate as soon as the twenty-fifth vertebra is incorporated in the sacrum. So that in this specimen we have the foetal condition of the lumbar region persisting in the adult, and associated with a rudimentary first thoracic rib.

## ENDOPHLEBITIS.<sup>1</sup> By ARTHUR V. MEIGS. (PLATE LV.)

I SHALL relate the history of a patient and describe the appearances of a minute diseased vein that was removed from his foot. Disease of the veins has been by no means exhaustively studied, and the clinical history of the case is interesting, for it demonstrates that there was also extensive disease of the arteries. The word 'endophlebitis' has been used to describe the disease of the vein, although it is not a word which can be said to be in common use. This is not the invention of a new word, but simply the addition of a prefix to one which is in common use. The reason I have added the prefix is, because the term phlebitis is most often used in medicine to describe the disease which is commonly called 'milk leg,' and other inflammations of veins. Therefore, if I had called the disease of the vein phlebitis, it would probably have conveyed a wrong impression. Besides, the changes in the vein correspond almost exactly with the disease in arteries which is called endarteritis, and it seemed desirable to have a name which should stand in contrast with that of endarteritis, and thus call attention to the similarity of the disease of the two kinds of blood-vessels.

An Italian stone-mason, twenty-five years of age, was admitted to the Pennsylvania Hospital, February 27, 1899. There was no history of hereditary disease in his family. He had had syphilitic infection a year and a half ago, and he drank occasionally, but not to excess. He never was sick in his life until January, when he had an attack of sickness which he called 'grippe,' and which lasted two weeks; from this he recovered and returned to work. Ten days before coming to the hospital he was seized with vomiting and pain after drinking some beer. There was no diarrhoea, but the pain continued. It was in the epigastrium and in the chest and lumbar region, and there was præcordial distress, and at times shortness of breath and head-

<sup>1</sup> Read at the Meeting of the Pathological Society of Philadelphia, held Nov. 9, 1899.





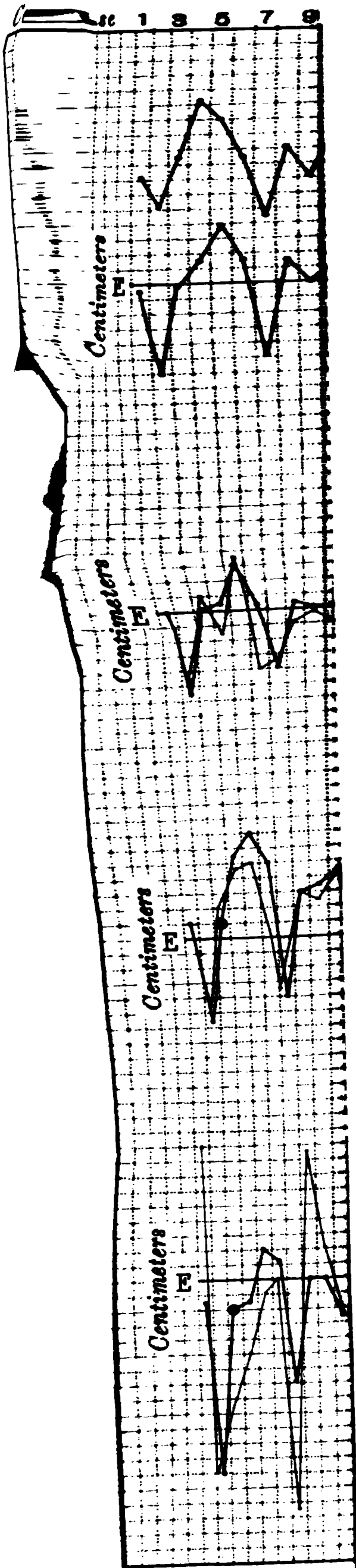


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ache, but no cough nor swelling of the feet. Physical examination gave the following results:—The heart action was slow and exceedingly irregular, but not tumultuous. There was no evidence of cardiac enlargement nor of valvular disease. Often when the heart-beat was irregular if he lay in bed, it would become regular if he sat up. The radial arteries felt stiffer than natural, the right more than the left, and their pulsation was visible. The ulnars, temporals, carotids, and femorals seemed to be natural. The left dorsalis pedis pulsated visibly and felt very thick, but there was no discoverable disease of the right. A small vein which extended across the right foot about an inch from the roots of the toes, and which received branches from the superficial veins of the toes, could be felt to be distinctly thickened. As this vein lay directly beneath the skin its unnatural thickness could easily be distinguished by passing the finger back and forth across it, especially where it crossed the tendons, which made a firm background against which to press it. It felt like a minute cord instead of almost disappearing when compressed, as a healthy vein will do when felt through the skin. The corresponding vein of the left foot also was much thicker than natural, but less than the one that has been described. As the patient said he was quite willing, a short incision was made through the skin, and a small piece of the thickened vein was removed from the right foot. In the removal blue venous blood was seen in the vessel, proving that it was a vein. When the cut end of the vein was examined with a hand lens, it was seen to be almost solid; there remained only a very small opening. Examination of the lungs, liver, spleen, and abdomen was quite negative, and there was no evidence of any cerebral disease. The urine was examined several times and nothing unnatural found. When first admitted to the hospital the patient was put to bed and given digitalis, as it was thought he was suffering more from heart disease than from anything else. As he improved but little, he was afterwards given salicylates and then put upon alkaline treatment, and later iodides were tried. Sometimes he was kept in bed, and at others was allowed to be up and about the ward. No treatment afforded more than temporary relief, and at the end of two months he was still suffering with constant pain in the

chest and down the arms, this being so severe that he said he slept very little. The heart action was always slow and irregular. At the end of two months he was lost sight of, and nothing is known of the subsequent history.

The illustrations are etchings which were made with the camera lucida; the images of the objects under the microscope were reflected directly upon the steel plate, and drawn with the needle. They are therefore, as nearly as possible, correct in dimension and detail. The pictures are of two sections of the vein from the right foot, and the parts represented were separated by less than a quarter of an inch. Both views show the vessel to be almost closed. The vein appears as a nearly solid cord, instead of being a thin-walled tube, as natural veins are. The material filling the calibre is represented in the two pictures as being very different. In the upper one there is a good deal of thickening of the intima, but much the greater part of the thickened tissue is the muscular coat, outside of which is the adventitia, which presents no evidence of disease. The intima is composed of fibrous tissue, in which the nuclei are easily distinguished, and the small slit-shaped opening is lined by a fringe of endothelial nuclei. Such an appearance of the intima and of the calibre is common in diseased arteries. The muscular wall, on the other hand, which occupies quite two-thirds of the entire thickness of the vessel wall, is unlike anything that I have previously seen in diseased blood-vessels. Although it is correct to call it the muscular coat, by no means all of it is muscular tissue. The muscle fibres, with their long, narrow nuclei, are well represented in the drawing; but it is also seen that the bands have been separated and thrown into wavy lines by a material which has grown in the midst of the muscular tissue, and has distorted it. This tissue is represented by the lighter coloured areas in the picture, and they also contain many nuclei, but these are different in appearance from the muscular nuclei. Evidently a morbid fibroid tissue has grown in the muscularis, and at its expense. The appearances here represented are a more graphic demonstration than anything I have previously met that it is an error to call this increase of thickness of the muscular coat a hypertrophy, as is commonly said of it when it occurs in arteries, and that it is unreasonable to believe it can add to the power

of useful contractility of vessels. The lower picture is very different from the upper one, but a careful examination of it reveals that the disease which distorted the two parts of the vein had worked in a somewhat similar manner in both parts. The most striking characteristic is the large knots of twisted tissue which fill up a great part of the calibre of the vein. These masses resemble the knots that are formed by a large number of earthworms together, and they are the result of a growth of the intima, which was so rapid as to outstrip the growth of other parts of the vein, so that the calibre could contain them only when coiled and twisted.

There are parts of the calibre where the intima is moderately thickened and the endothelial cells are distinct in places, but they are generally somewhat enlarged and more rounded than is natural, and few, if any, of them appear as flat plates upon the inner side of the vessel. There is great thickening of the muscular coat, but this is less in degree than that represented in the upper picture; and in places the muscularis and intima run together in such a way that it is impossible to say where the one ends and the other begins. The disease has gone so far that the muscular tissue bears little resemblance to natural muscle, and the intima as little to the natural intima of veins. Disease often totally changes the appearance of tissues, and this reminds one that at early embryological stages the various organs are so much alike that they can be recognised with the microscope only by their situations, and not by the arrangement or appearance of their cells. It seems as if disease is sometimes of the nature of a retrogression. The diseased tissues lose their natural characteristics, and fall back toward the lack of differentiation which is natural in the tissues of early embryos. The cause which seems to have the greatest influence in bringing about this retrogression is the growth of morbid fibroid tissue. In the forms of disease represented by the two pictures, the most striking feature in both is the growth of morbid fibroid tissue in the intima and in the muscularis.

The disease that has been described, and which is shown by the pictures, would be attributed by most persons to syphilis, as the patient said he had been infected, and this explanation would generally be considered to be satisfactory and conclusive. It

may be that the disease was syphilis, and there is no other cause at hand which better explains the disease of the vein, the extensive endarteritis, and the disease of the heart which the physical examination of the patient demonstrated. There is good reason for believing that syphilis produces such vascular disease, but it would be a mistake to suppose that syphilis only can cause it. I know that such is not the case, as I have in my possession sections of the radial artery of a negro man of twenty-four years of age, who died of tabes mesenterica and pulmonary tuberculosis, which are in a similar state of disease. There is the same overgrowth of the intima and the formation of convolutions, and the muscular coat is thick and the calibre nearly closed. I have also sections of the radial vein of a boy of fifteen who died of meningitis, after an illness of about three months, and these show similar disease. It is not uncommon to find the muscular coat of the radial veins thickened and the fibres separated by the growth of morbid fibroid tissue in persons whose radial vessels had been felt during life to be thickened. In my book on the *Origin of Disease*<sup>1</sup> there is a picture of a portion of vena cava of a man, fifty-seven years old, who died of Bright's disease, which shows thickening of the muscular coat and separation of its fibres. Since similar changes of the veins have been found in persons suffering with other diseases, and who were not syphilitic, it would be an error to emphasise too much the fact that in the case under consideration the patient had been infected with syphilis. It is now well known that the form of endarteritis which used to be considered to be syphilitic, arises also from a variety of other causes. Diseases of veins have not yet been very thoroughly studied, by no means so thoroughly as arterial disease, and it is probable that the veins are much more subject to disease than is now known. The opportunity afforded by the case that has been narrated was exceptional, as the vein was obtained during the life of the patient, and it was possible to be certain that it was a vein, otherwise it would very probably have been mistaken for an artery, as there is nothing to distinguish the two sorts of vessels when they are diseased. It is probable that there is something in the nature of the muscularis of veins that makes it peculiarly

<sup>1</sup> *The Origin of Disease*, by Arthur V. Meigs, p. 59, and fig. 36.

liable to such disease as that shown by the plate. I have never seen anything exactly like it in the muscularis of an artery.

Nothing has yet been said of the clinical aspect of the case, although it is as valuable clinically as it is pathologically; but the results of clinical study are less certain and graphic.

The case was one of disease of the heart and of the blood-vessels. My experience has taught me to believe that it is rare for one of the great organs to be diseased and the others to remain healthy. Even when there is clinical evidence of disease of only one organ, others are generally involved. This I have learned from the study of pathology, for I have generally found that in cases which during life had been recognised from the symptoms as instances of heart disease or of kidney disease, there was disease of other organs, which was easily recognised if it was sought for after death. It is, therefore, highly probable that in the case under consideration there was more disease than was revealed by the history of the patient and the physical examination. The disease of one vein of the right foot has been described, and it is certain that there was similar disease of the corresponding vein of the other foot, for it also was stiff. It was mentioned that a number of the arteries were seen to pulsate visibly and were felt to be stiff. These are certain indications of disease, and I speak so positively because I have frequently made microscopical examinations after death of arteries that I had ascertained during life to be stiffened and to pulsate visibly, and invariably I have found disease. It has been said that there was disease of the heart, and I feel sure that such must have been the case, although the evidences of this were only the slowness and irregularity of the beat and the pain in the chest, in the præcordial region, and down the arm. Even in the absence of any direct physical sign of cardiac enlargement or of valvular disease, I am certain there must have been grave organic disease of the heart. Probably it was degeneration of the muscular tissue, and it was this heart disease that was the true cause of the man's symptoms and disability, rather than the disease of the blood-vessels or any other undiscovered lesion. Thus the case is clinically an interesting one, but the lessons which are taught by it clinically are less striking than those which its pathology teaches.

## DESCRIPTION OF PLATE LV.

(The scale on the Plate applies to the figures A and B.)

A ( $\times 56$ ).—Section of vein almost closed by thickening of the muscularis. The thickened muscularis is only partly composed of true muscular tissue; which has been torn apart and thrown into wavy strands by morbid fibroid tissue which has grown in it.  $x$ , the line of separation of the fibrous coat from the muscularis;  $y$ , the line of separation of the muscularis from the intima. All the tissue between  $x$  and  $y$  is muscularis; the thickening is very great. At  $y$  the separation of muscularis from intima is clearly marked, but at other parts of the circuit there is no distinguishable boundary-line. The intima is much thickened, but not so much as the muscularis. The calibre is beaded with endothelial nuclei.  $z$  is an area represented more highly magnified by D.

B ( $\times 56$ ).—Another section of the same vein, showing also great thickening of the walls, but of a different character. The opening is almost filled by irregular projections from the intima. One of these ( $o$ ) is composed of the plicated membrane, which is curiously folded and knotted. There is another somewhat similar knot of smaller size, and several irregularly-shaped projections of the intima, which fill a large portion of the calibre. The muscularis is irregularly thickened. Parts of it are hard to recognise as involuntary muscle, being more like morbid fibroid tissue.  $p$  is distinctly muscular tissue.  $m$  shows the muscularis and intima shading together without a distinguishable line of separation.  $n$  marks a spot where the separation of the two coats is distinct.

C ( $\times 220$ ).—A portion of the muscularis from A, more highly magnified. It shows the character of the long and narrow nuclei of the involuntary muscle.

D ( $\times 220$ ).—The region  $z$  from A, more highly magnified. The central portion is morbid fibroid tissue, showing a fine mesh and containing a single connective-tissue nucleus. Outside of this is muscular tissue containing the elongated muscular nuclei. This shows the manner in which the muscular tissue is torn apart by the growth of the morbid fibrous tissue.







ON THE ORIGIN OF VERTEBRATES, DEDUCED FROM  
THE STUDY OF AMMOCETES. By WALTER H.  
GASKELL, M.D., LL.D., F.R.S., *University Lecturer on  
Physiology; Fellow of Trinity Hall, Cambridge.* PARTS  
V., VI., VII., VIII. (PLATES LVI., LVII.)

PART V.—ON THE ORIGIN OF THE PRO-OTIC SEGMENTATION; THE  
MEANING OF THE TRIGEMINAL AND EYE-MUSCLE NERVES.

IN my last paper I completed the history of the cranial nerves which supplied the branchial segments, *i.e.*, of the nerves which, according to my theory, originally supplied mesosomatic appendages; I now come to the consideration of the nerve group in front of these nerves, *i.e.*, the trigeminal nerve group, or the pro-otic segmental nerves; nerves which, according to the theory, formed originally the group of prosomatic nerves. This group consists of the trigeminal as the nerve supplying the visceral or splanchnic segments with motor fibres, and the eye-muscle nerves supplying the corresponding somatic segments, while the trigeminal supplies both the somatic and splanchnic segments with sensory fibres, with the exception of the eye-muscles themselves. In accordance, then, with the nerves of the branchial segments, it follows that the muscles supplied by the motor part of the trigeminal ought to have originally moved the appendages belonging to a series of prosomatic segments, and therefore we may expect to find evidence of such appendages in the lowest vertebrate. On the other hand, the eye-muscles ought to have originally belonged to the prosomatic segments themselves, and must therefore have been grouped originally in a segmental series corresponding to the prosomatic appendages.

*The Prosomatic Appendages of the Merostomata.*

IN order to make the problem quite clear to the minds of my readers, it is advisable to sketch out the nature of the prosomatic segments and appendages in the Merostomata before proceeding

to the description of the peculiarities of this region as seen in *Ammocoetes*, so as to show what we might reasonably expect to find in *Ammocoetes*, if in this region, as in the opisthotic or mesosomatic region, it is possible to institute a direct comparison between *Ammocoetes* and these old-world scorpion forms.

In all this group of animals the evidence of the number of segments in either the prosomatic or mesosomatic regions is given by—

1. The number of appendages.
2. Apart from the appendages, the segmental arrangement of the muscles of the prosoma or mesosoma respectively.
3. The segmental arrangement of the coelomic or head cavities.
4. The divisions of the central nervous system or neuromeres, together with their outgoing segmental nerves.

It follows, therefore, that if from any cause the appendages are not apparent, as in many fossil remains, or have dwindled away and become insignificant, we still have the muscular, coelomic, and nervous arrangements left to us as evidence of segmentation in these animals, just as in vertebrates.

In this prosomatic region we find in *Limulus* the same tripartite division of the nerves as in the mesosomatic region, so that the nerves to each segment may be classed as (1) appendage nerve; (2) sensory or dorsal somatic, supplying the prosomatic carapace; (3) motor or ventral somatic, supplying the muscles of the prosoma, and containing possibly some sensory fibres. The main difference between the two regions in *Limulus* consists in the closer aggregation of the prosomatic nerves, corresponding to the concentration of the separate ganglia of origin in the prosomatic region of the brain.

The number of prosomatic segments in *Limulus* is not evident by the observation of the prosomatic carapace, so that the most reliable guide to the segmentation of this region is given by the appendages, of which one pair corresponds to each prosomatic segment.

The number of such segments, according to present opinion, is seven, viz. :—

- (1) The foremost segment, which bears the chelicerae;
- (2, 3, 4, 5, 6) The next five segments, which carry the paired locomotor appendages; and

(7) The last segment, to which belongs a small, abortive pair of appendages known by the name of the chilaria, situated between the last pair of locomotor appendages and the operculum or first pair of mesosomatic appendages. These appendages are numbered from 1-7 in the accompanying drawing (fig. 1).

Of these seven pairs of appendages the signification of the first and the last has been matter of dispute. With respect to

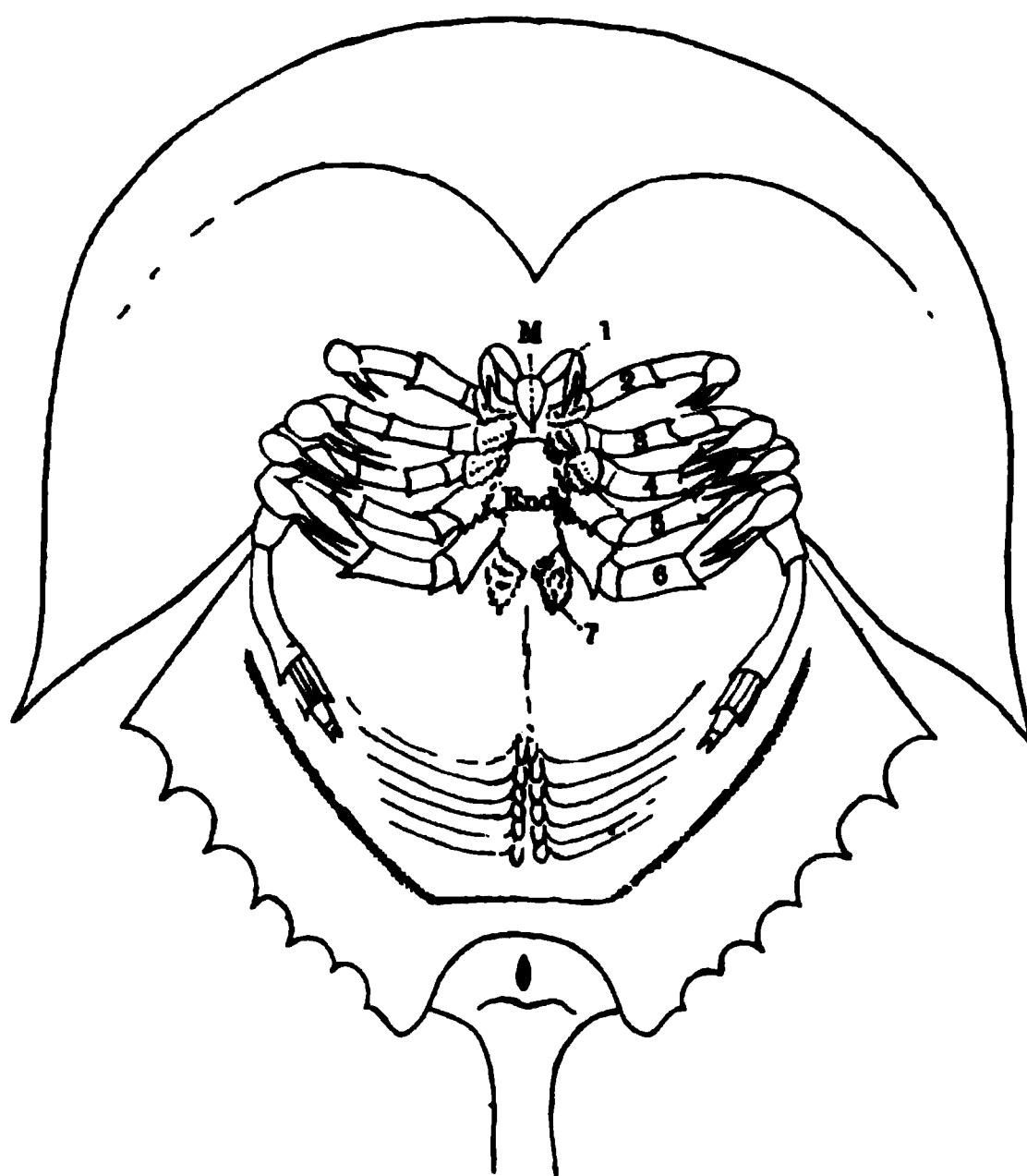


FIG. 1.—Ventral surface of *Limulus* (taken from Kishinouye). The gnathic bases of the appendages have been separated from those of the other side to show the promesosternite or endostoma (End.).

the first pair, or the chelicerae, the question has arisen whether their nerves belonged to the infra-oesophageal group, or were in reality supra-oesophageal.

It is instructive to see the nature and the anterior position of this pair of appendages in the allied sea scorpions, especially in *Pterygotus*, where the only chelate organs are found in these long, antenna-like chelicerae. In *Slimonia* and in *Stylonurus*

they are supposed by Woodward<sup>1</sup> to be represented by the small non-chelate antennæ seen in figs. 2 B and C, taken from Woodward.

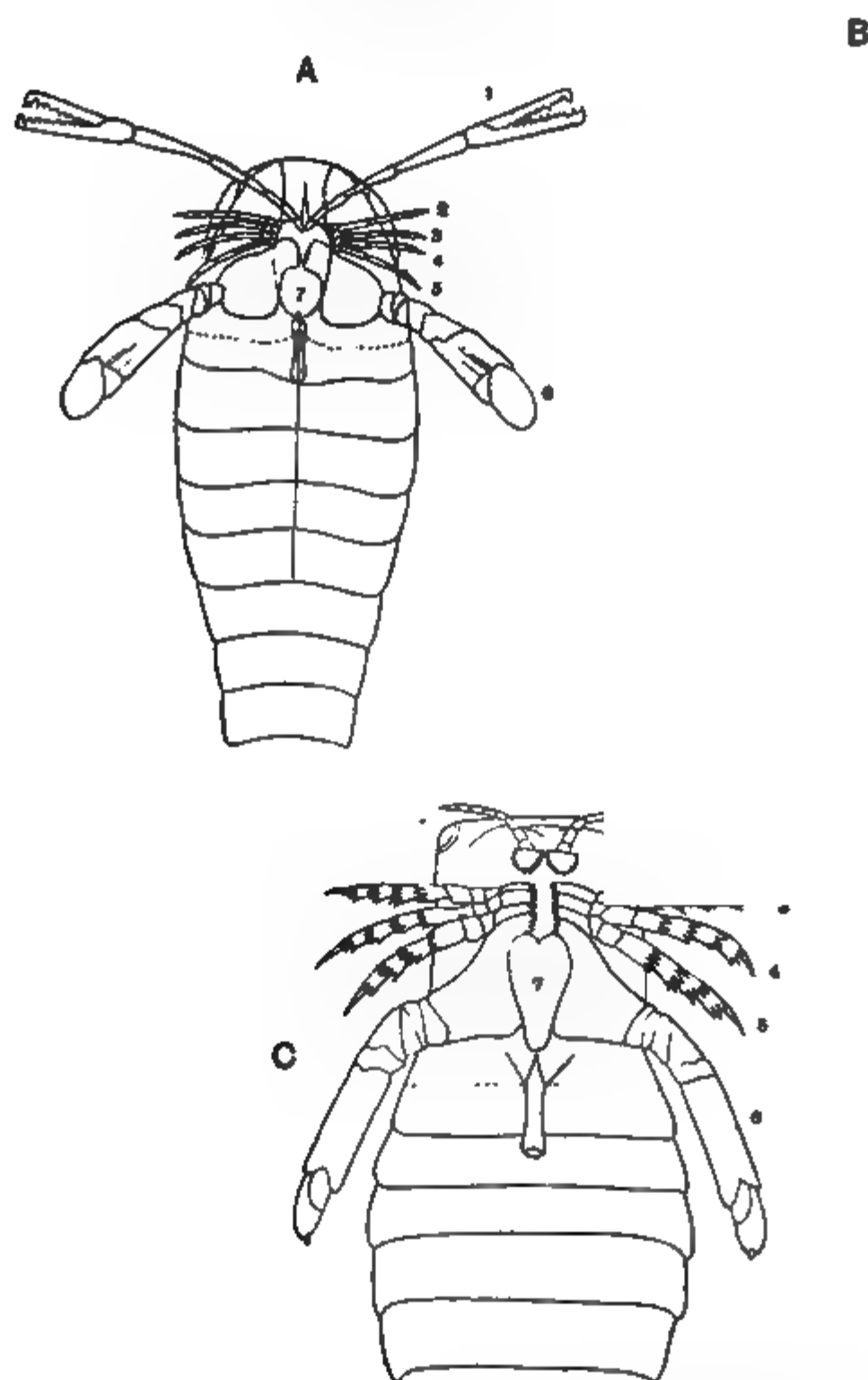


FIG. 2.—A, *Pterygotus Oalliensis* (from Schmidt.  
B, *Stylonurus Loganii* (from Woodward).  
C, *Slimonia acuminata* (from Woodward).

If such is the case, then these figures show that a pair of appendages is missing in each of these forms, for they possess only five

<sup>1</sup> "A Monograph of the British Fossil Crustacea, belonging to the order Merostomata," by H. Woodward, Paleontographical Society, 1878.

free prosomatic appendages instead of six, as in *Limulus* and in *Pterygotus*. Similarly, Woodward only allowed five appendages for *Pterygotus*, so that his restorations were throughout consistent. Schmidt<sup>1</sup> in *Pterygotus osiliensis* has shown that the true number was six, not five, as seen in his restoration given in fig. 2, A.

With respect to *Eurypterus*, Schmidt figures an exceedingly fine pair of antennæ between the coxal joints of his first pair of appendages, thus making six pairs of appendages. Gerhard Holm,<sup>2</sup> however, in his recent beautiful preparations from Schmidt's specimens and others collected at Rootziküll, has proved most conclusively that the chelicerae of *Eurypterus* were of the same kind as those of *Limulus*. I reproduce his figure on the next page,—the small chelate chelicerae overhanging the mouth orifice just as in *Limulus* or in *Scorpio*.

So also, since Woodward's monograph, Laurie<sup>3</sup> has discovered in *Slimonia acuminata* a small median pair of chelate appendages, exactly corresponding to the chelicerae of *Limulus*, or of *Eurypterus*, or of *Scorpio*. We may therefore take it for granted that such was also the case in *Stylonurus*, and that the foremost pair of prosomatic appendages in all these extinct sea scorpions were in the same position and of the same character as the chelicerae of the scorpions.

In the living scorpion and in *Limulus* the nerves to this pair of appendages undoubtedly arise from the foremost prosomatic ganglia, and the reason why they appear to belong to the supra-oesophageal brain mass has been made clear by Brauer's<sup>4</sup> investigations on the embryology of *Scorpio*; for he has shown that the chelicerai ganglia shift from the ventral to the dorsal side of the oesophagus during development, thus becoming pseudo-supra-oesophageal, though in reality belonging to the infra-oesophageal ganglia. This chelicerai pair of appendages is in all

<sup>1</sup> "Die Crustaceen fauna der Eurypteren schichten von Rootziküll auf Oesel," Fr. Schmidt, *Mem. d. l'Acad. Imp. d. Sci. d. St Petersburg*, vii. ser. t. xxxi., 1883.

<sup>2</sup> "Ueber die Organisation d. *Eurypterus Fischeri*," Gerhard Holm, *Mem. d. l'Acad. Imp. d. Sci. d. St Petersburg*, viii. ser. vol. viii., 1898.

<sup>3</sup> "The Anatomy and Relations of the Eurypteridæ," by M. Laurie, *Trans. of Royal Soc. Edin.*, vol. xxxvii., 1893.

<sup>4</sup> "Beiträge zur Kenntniss d. Entwicklungsgeschichte d. Skorpions II.," A. Brauer, *Zeitsch. f. Wissensch. Zool.*, vol. 59, p. 418, 1895.

probability homologous with the second pair of antennæ in the Crustacea.

I conclude, then, that the chelicerae must truly be included in the prosomatic group, but that they stand in a somewhat different category to the rest of the prosomatic appendages, as they take up a very median, anterior, and somewhat dorsal position, and their ganglia of origin are also exceptional in position.

Next for consideration come the chilaria (7 in fig. 1), which Lankester<sup>1</sup> did not consider to belong to appendages at all, but to be a peculiar pair of sternites. Yet the very appear-

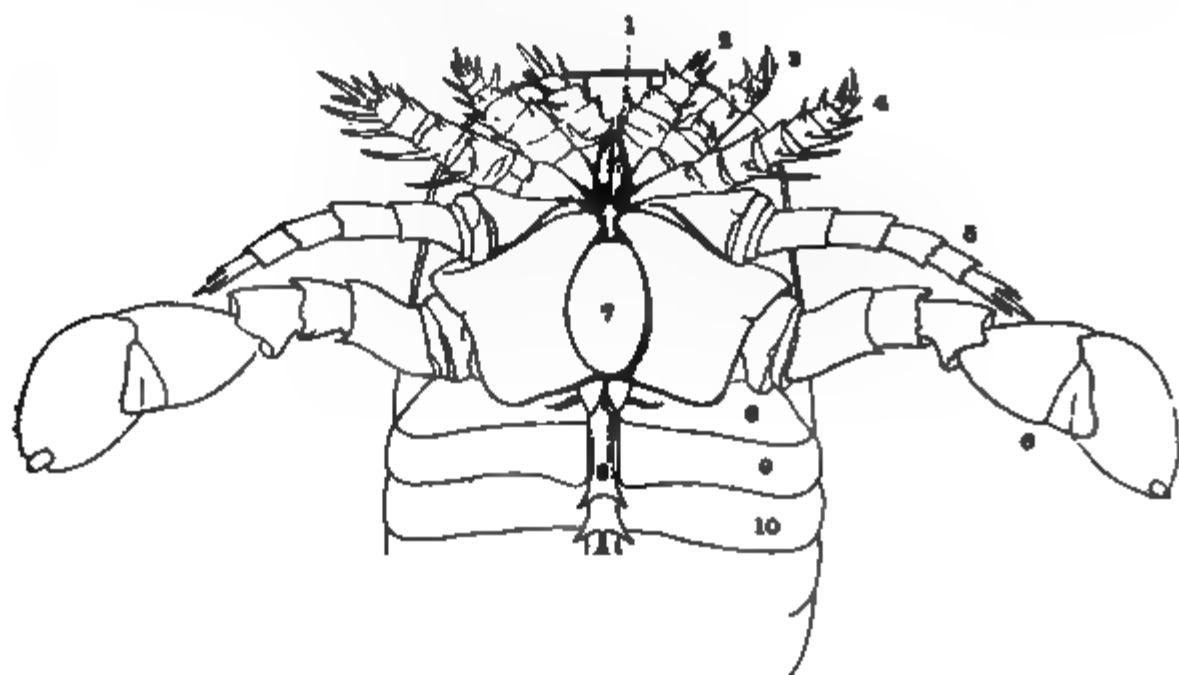


FIG. 3.—*Eurypterus Fischeri* (from Holm).

ance of them, with their spinous hairs corresponding to those of the other gnathites and their separate nerve supply, all point distinctly to their being a modified pair of appendages, and indeed the matter has been placed beyond doubt by the observa-

<sup>1</sup> "Limulus an Arachnid," by E. Ray Lankester, *Q. J. Micr. Sci.*, vol. xii, p. 504, 1881.

tions of Kishinouye,<sup>1</sup> who has found embryologically that they arise in accordance with the rest of the prosomatic appendages, and belong to a distinct prosomatic segment, viz., the seventh segment. In accordance with this, Brauer<sup>2</sup> has found that in the scorpion there is in the embryo a segment, the appendages of which degenerate, which is situated between the segment bearing the last pair of thoracic appendages and the genital operculum,—a segment therefore comparable in position to the chilarial segment of *Limulus*.

This last segment and last prosomatic appendage is especially interesting, because in all the old sea scorpions a structure is invariably found in this position, which is considered to be homologous with this seventh pair of prosomatic appendages. This structure is known by the name of the metastoma or lip-plate. It is numbered 7 in figs. 2 and 3, and in all cases was a median single plate situated externally, which covered the basal joints of the last pair of locomotor appendages.

Until quite recently it would have been difficult to be quite certain that the metastoma formed the ventral wall of a prosomatic chamber, as I supposed, in my address at Liverpool in 1896, must have been the case, if the metastoma was formed by the fusion and forward growth of the chilaria. Now, however, the relations of the metastoma to the parts about the mouth are made quite clear by the beautiful researches of Holm,<sup>3</sup> from which it is evident that this last pair of prosomatic appendages does form the ventral wall of a prosomatic chamber of the very kind postulated by me. As I am here considering only the appendages and not the mouth parts of the Merostomata, I will leave the further consideration of Holm's researches until Part VI., which deals with the old mouth and the olfactory nerve.

I conclude from the evidence that the metastoma represented the fused last pair of prosomatic appendages, and so formed a ventral lip to a prosomatic or oral chamber.

Moreover, seeing that the metastoma was not a surface plate, but was formed by the fusion of a pair of appendages, it follows

<sup>1</sup> "On the Development of *Limulus Longispina*," by K. Kishinouye, *Journ. of Coll. of Science, Imp. Univ., Japan*, vol. v., 1891.

<sup>2</sup> *Op. cit.*, p. 360-363.

<sup>3</sup> *Op. cit.*

necessarily that its basal part must have been fused to the basal part of the operculum ; so that, between the common genital and respiratory chamber described in Part IV. of this series of papers and the prosomatic or oral chamber, a septum must have existed composed of the basal portion of the opercular and metastomal appendages. In this septum the nerves to the last prosomatic appendage (equivalent to the last part of the trigeminal in the vertebrate) and to the first mesosomatic (equivalent to the thyroid part of the facial) would run as shown in fig. 17, B, close together in the first part of their course, and would separate when the ventral surface was reached to pass headwards and tailwards respectively.

Coming now to the five locomotor appendages, we find that they resemble each other to a considerable extent in most cases, with, however, certain striking differences ; thus in *Limulus* they are chelate, with their basal joints formed as gnathites, except in the case of the fifth appendage, in which the extremity is modified for the purpose of digging in the sand.

In *Pterygotus*, *Slimonia*, *Eurypterus*, the first four of these appendages are very similar, and are called by Huxley and Woodward endognaths ; in all cases they possess a basal part or sterno-coxal process which acts as a gnathite or foot-jaw, and a non-chelate tactile part, which possesses no prehensile power, and in most cases could have had no appreciable share in locomotion, called by Huxley and Woodward the palpus. These small palps were probably retractile, and capable of being withdrawn entirely under the hood. The fifth appendage is usually different, being a large swimming organ in *Pterygotus*, *Eurypterus*, and *Slimonia* (figs. 2 and 3), and is known as the ectognath.

Finally, in *Drepanopterus Bembycoides*, as stated by Laurie,<sup>1</sup> all five locomotor appendages are built up after the same fashion, the last one not being formed as a paddle-shaped organ or elongated as in *Stylonurus*, but all five possess no special locomotor or prehensile power. According to Laurie this is a specially primitive form of the group.

It is significant to notice from this sketch that with the

<sup>1</sup> Laurie, "On a Silurian Scorpion and some additional Eurypterid Remains from the Pentland Hills," *Trans. Roy. Soc. Edin.*, vol. xxxiv. p. 584, 1899.



absence of special prehensile terminations such as chelæ, or the absence of special locomotor functions such as walking or swimming, these appendages tend to dwindle and become insignificant, taking up the position of mere feelers round the mouth, and at the same time are concentrated and pressed closely together, so that their appendage nerves must also be close together.

As far, then, as the prosomatic appendages and their nerves are concerned, this sketch causes us to conclude that the primitive form which gave rise to the vertebrates may have been a still simpler form of a Eurypterus-like animal which possessed a prosomatic chamber formed by a metastoma or accessory lip, within which were situated five pairs of short tactile appendages or tentacles. In such case the trigeminal nerve, as the representative of these prosomatic appendage nerves, ought to be found to supply the muscles of this accessory lip and of these five pairs of tentacles in the lowest vertebrate. With the evidence of the appendages themselves we do not complete the evidence of the number of segments in the prosomatic region due directly to the presence of the appendages, for we see that the prosomatic region of the central nervous system in all the scorpion group is divided into well-defined neuromeres in accordance with the appendages, a segmentation the reminiscence of which may still persist after the appendages themselves have dwindled or disappeared, and thus give rise to the neuromeres of the American writers.

We also see that under the prosomatic carapace are attached a regular series of muscles directly connected with the coxal joint of each appendage, called by Lankester tergo-coxal muscles, so that in this system of muscles we have further evidence of the segmentation of this prosomatic region due directly to the appendages.

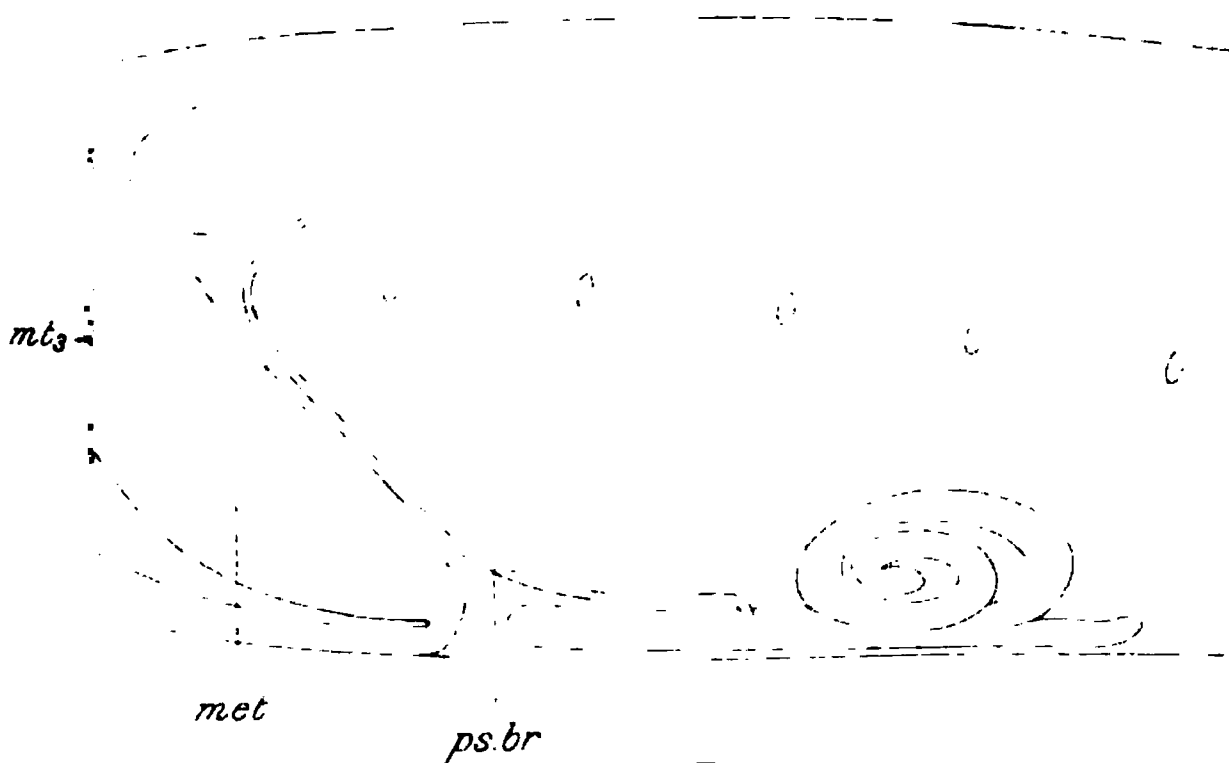
The evidence of the muscular system of *Limulus* and *Scorpio* is given by the researches of Benham and Miss Beck under Lankester's direction.<sup>1</sup> From these researches Lankester concludes that the simple musculature of the primitive animal from which

<sup>1</sup> "On the Muscular and Endo-skeletal Systems of *Limulus* and *Scorpio*," by E. Ray Lankester, assisted by W. B. S. Benham and Miss E. J. Beck, *Zool. Trans.*, vol. xi. p. 311, read 1883.

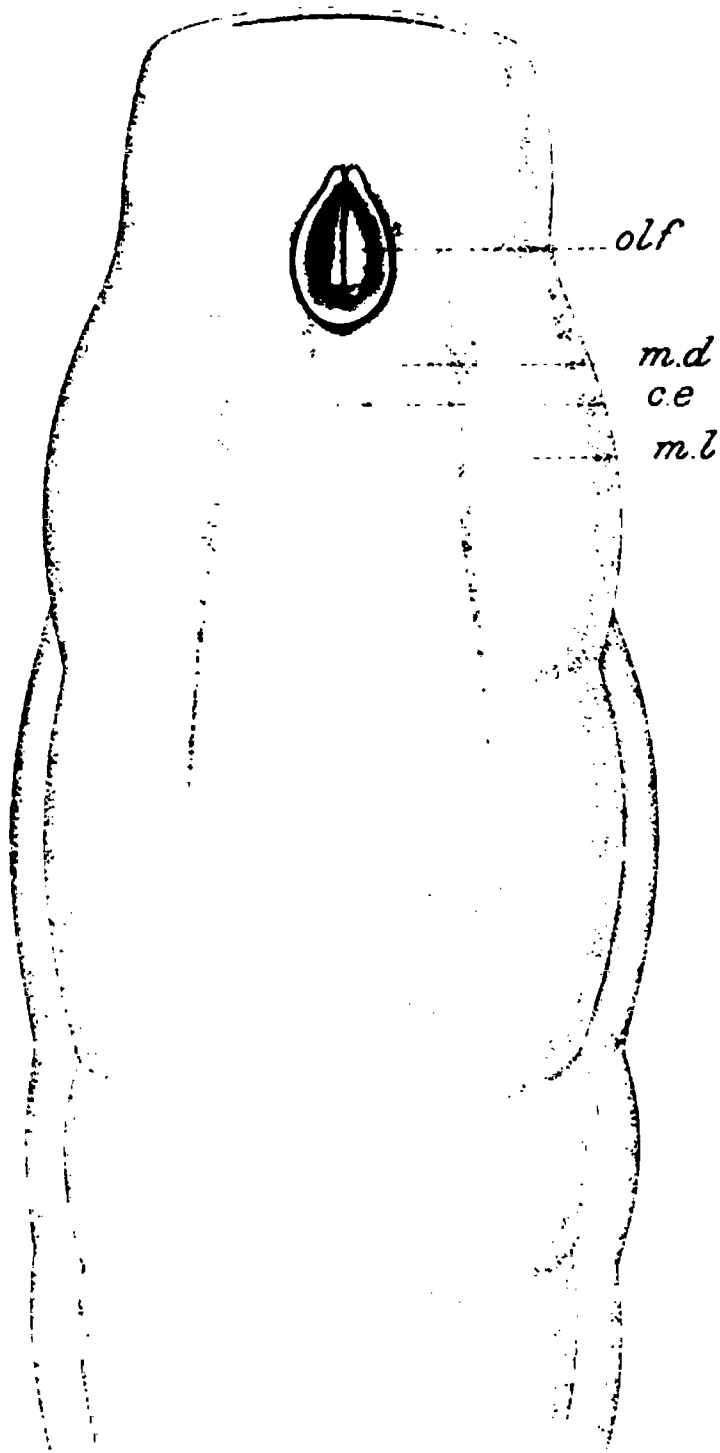
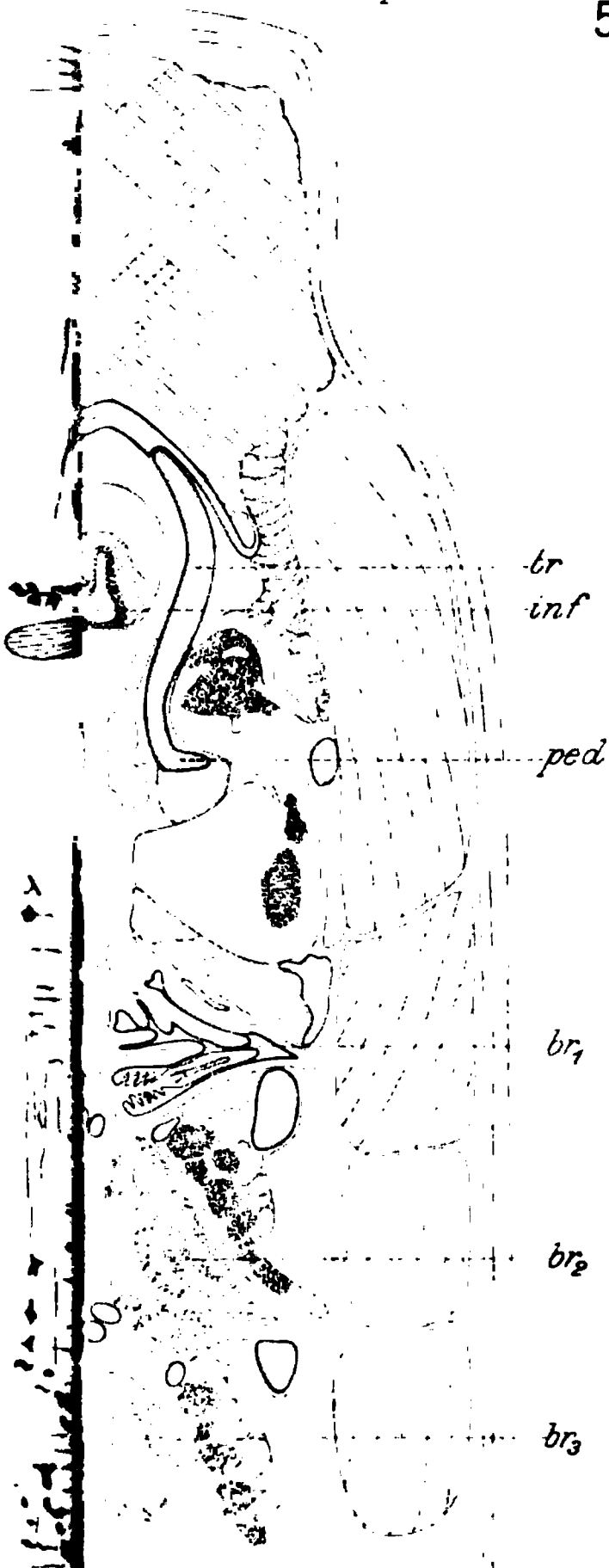
both *Limulus* and the scorpions arose consisted of (1) a series of paired, longitudinal, dorsal muscles passing from tergite to tergite of each successive segment; (2) a similar series of paired, longitudinal, ventral muscles; (3) a pair of dorso-ventral muscles passing from tergite to sternite in each segment; (4) a set of dorso-ventral muscles moving the coxa of each limb in its socket; (5) a pair of veno-pericardial muscles in each segment. Of these muscles, the dorso-ventral ones alone give evidence of the number of segments in the prosomatic region of *Limulus* and the scorpions, especially the large, segmentally-arranged tergo-coxals, which in *Limulus* pass in regular sequence from the dorsal carapace to the coxa of each prosomatic appendage on the same side.

Of these the tergo-coxal muscles of the first pair of appendages or chelicerae is attached to the carapace nearer the middle line and separate from the more laterally attached large muscles of the 2nd, 3rd, 4th, 5th, 6th appendages.

In *Mygale* these large tergo-coxal muscles are somewhat radially arranged, and it is striking to see how the prosomatic carapace is distinctly marked out on its external surface in correspondence with these muscles, so that in this case the segmentation of the prosomatic region is distinct on the external carapace as a radial series of elevations and depressions, owing to the strong aponeurotic attachments between the tergo-coxal muscles; and if such a carapace alone was found in a fossil condition, we should know that the animal to which it belonged possessed a corresponding number of prosomatic appendages. Similarly, in *Phrynus*, the prosomatic carapace is marked out more or less distinctly, in accordance with the appendages, as is seen in fig. 4, which represents the external surface markings. Upon removing the carapace, the arrangement of the aponeurotic bands between the tergo-coxal muscles to which the external markings are due are well seen, as in fig. 5. I venture, then, to suggest that in those forms which are only known to us in the fossil condition, in which no prosomatic appendages have been found, but which possess, more or less clearly, radial markings on the prosomatic carapace resembling those of *Phrynus* or *Mygale*, such radial markings may be interpreted as due to the presence of prosomatic

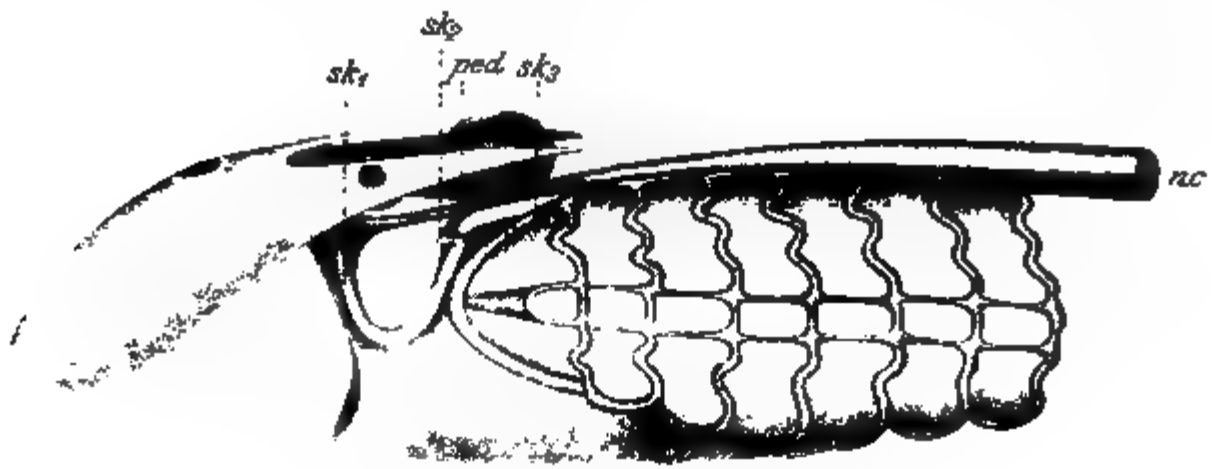


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appendages which are either entirely concealed by the prosomatic carapace or dorsal head-plate, or were of such a nature as not to have been capable of fossilisation.

In connection with this suggestion, I should like to point out here, that throughout this series of papers, although I have spoken chiefly of *Limulus*, *Eurypterus*, and the modern Scorpion group, I have never supposed that any one of these animals was the actual ancestor of the vertebrates; I have simply meant that the ancestor must be sought for among that large group of extinct animals allied, on the one hand, to *Limulus* and the

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FIG. 4.—*Phrynos Margine-Maculata*. Ce, median eyes; le, lateral eyes; glab, median plate over brain; Fo, fovea.

Scorpions, and on the other, to the Trilobita, which were the dominant race of animals in the Upper Silurian waters at the time when the earliest known fishes made their appearance.

This group of animals forms the great group of chiefly extinct animals classified by H. Woodward<sup>1</sup> under the order *Merostomata*. They are divided by him into the sub-order *Eurypteridæ*, which include—(1) *Pterygotus*, (2) *Slimonia*, (3) *Stylonurus*, (4) *Eurypterus*, (5) *Adelophthalmus*, (6) *Bunodes*, (7) *Arthropleura*, (8) *Hemiaspis*, (9) *Exapinurus*, (10) *Pseudoniscus*; and the sub-order *Xiphosura*, which include—(1) *Belinurus*, (2) *Prestwichia*, (3) *Limulus*.

The evidence of the *Xiphosura* and of the *Hemiaspidæ* con-

<sup>1</sup> *Op. cit.*

clusively shows, in Woodward's opinion, that the Merostomata are closely related to the Trilobite, and the Hemiaspidæ especially are supposed to be intermediate between the Trilobites and the King-crabs. They are characterised, as also *Belinurus* and *Prestwichia*, by the absence of any prosomatic appendages, so that in these cases, as is seen in fig. 6 representing *Bunodes lunula*, from Schmidt,<sup>1</sup> found in the Eurypterus layer at Rootziküll,

supr oes

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FIG. 5.—*Plirynus* sp. (?). Carapace removed. cam, camerostome ; pl, plastron.

we have an animal after the *Limulus* fashion in which the prosomatic appendages have either dwindled away and are completely hidden by the prosomatic carapace, or become so soft as not to be preserved in the fossilised condition. The appearance of the prosomatic carapace is, to my mind, suggestive of the presence of

<sup>1</sup> *Op. cit.*



such appendages, for it is marked out radially as is seen in the figure in a manner resembling somewhat the markings on the prosomatic carapace of *Mygale* or *Phrynus*; these latter markings, as already mentioned, are due to the aponeuroses between the tergo-coxal muscles of the prosomatic appendages which lie underneath and are attached to the carapace.

A very similar radial marking is shown by Woodward<sup>1</sup> in his picture of *Hemiaspis Limuloides*, reproduced in fig. 7, found in the Lower Ludlow beds at Leintwardine. This species has

FIG. 6.—*Bunodes lunula* (from Schmidt).

given the most perfect specimens of the genus *Hemiaspis*, which is recognised to differ from *Bunodes* in the possession of a telson.

Such markings as indicative of the segmentation of the prosomatic carapace are, as we shall see later, very suggestive when we come to consider the similar evidences of segmentation in the head region of the earliest known fishes as given by Rohon.

*Evidence of Segmentation given by the Muscles of the Prosomatic Segments themselves.*

Next for consideration, as evidence of segmentation in the prosomatic region, come the dorso-ventral somatic muscles. These muscles, as already mentioned in Part III. of this series of papers, are most markedly segmental in the mesosomatic region both in *Limulus* and in *Scorpio*; each mesosomatic segment possessing a single pair of these vertical mesosomatic muscles, as Benham calls them. In the prosomatic region the

<sup>1</sup> *Op. cit.*, p. 177.

corresponding muscles are not so clearly defined in *Limulus*; they are apparently attached to the plastron forming the group of plastro-tergal muscles. From Benham's description it is evident enough that they formed originally a single pair to each prosomatic segment.

In *Scorpio*, according to Miss Beck,<sup>1</sup> the dorso-ventral prosomatic muscles are situated near the middle line on each side,

FIG. 7.—*Hemiaspis Limuloides* (from Woodward). gl, glabellum.

and form the following well-marked series of pairs of muscles shown in fig. 8A, taken from her paper, and thus described by her:—

1. The dorso-cheliceral-sternal muscle (61) is the most anterior of the dorso-ventral muscles; it is very small, and is attached to the carapace near the median line anterior to the central eyes.

2. The median dorso-preoral entosclerite muscle (62) is a large muscle, between which and its fellow of the opposite side

<sup>1</sup> *Op. cit.*

are situated the eyes; it is attached dorsally to the carapace and ventrally to the preoral entosclerite.

3. The anterior dorso-plastron muscle (63) is attached dorsally to the carapace in the middle line, being joined to its fellow of the opposite side. They separate, and are attached ventrally to the plastron. Through the arch thus formed pass the alimentary canal and the dorsal vessel.

4. The median dorso-plastron muscle (64) is attached dorsally to the posterior part of the carapace. It runs forward on the anterior surface of the posterior flap of the plastron to the body of the plastron, to which it is attached.

To these may be added, owing to its attachment to the plastron,—

5. The posterior dorso-plastron muscle (65) is the first of the dorso-ventral muscles attached to the mesosomatic tergites, being attached to the tergite of the first segment of the mesosoma.

This muscle is of interest, in connection with the prosomatic dorso-ventral muscles, because it is attached to the plastron, and runs a course in close contact with the muscle (64), the two muscles being attached dorsally close together, on each side of the middle line, the one at the very posterior edge of the prosomatic carapace, and the other at the very anterior edge of the mesosomatic carapace.

Taking these muscles separately into consideration, it may be remarked with respect to (1) that the cheliceral segment in its paired dorso-ventral muscles, as in its tergo-coxal muscles, takes up a separate position isolated from the rest of the prosomatic segments.

Next comes (2) the median dorso-preoral entosclerite muscle, which is strikingly different from all the other dorso-ventral muscles in its large size and the extent of its attachment to the dorsal carapace, according to Miss Beck's figures. The reason of its large size is clearly seen upon dissection of the muscles in *Buthus*, for I find that, strictly speaking, it is not a single muscle, but is composed of a series of muscle bundles, separated from each other by connective tissue. There are certainly three separate muscles included in this large muscle, which are attached in a distinct series along the preoral entosclerite, and present

the appearance given in fig. 8A at their attachment to the prosomatic carapace. Of this muscle group the most anterior and the most posterior bundle are distinctly separate muscles; I am not, however, clear whether the middle bundle represents one or two muscles.

This division of Miss Beck's muscle (62) into three or four muscles brings the prosomatic region of the scorpion into line with the mesosomatic, and enables us to feel sure that a single pair of dorso-ventral somatic muscles belongs to each prosomatic segment just as to each mesosomatic, and, conversely, that each such single pair of muscles possesses segmental value in this region as much as in the mesosomatic.

It is very striking to see how in all the Scorpionidæ, in which the two median eyes are the principal eyes, this muscle group (62) on the two sides closely surround these two eyes, so that with a fixed preoral entosclerite, a slight movement of the eyes, laterally or anteriorly, owing to the flexibility of the carapace, might result as the consequence of their contraction. Such cannot be the main object of these muscles. The preoral entosclerite is firmly fixed to the camerostome, as is seen in fig. 12, so that the main object of these muscles is, as Huxley<sup>1</sup> has pointed out, the movement of this organ.

In order to avoid the repetition of the long name given to this muscle group by Miss Beck, because of their position, and for other reasons which will appear in the sequel, I will call this group of muscles the group of recti muscles. These recti muscles belong clearly to the segments posterior to the first prosomatic or cheliceral segment, and represent certainly three, probably four, of these segments, *i.e.*, belong to the segments corresponding to the second, third, fourth, and fifth prosomatic locomotor appendages,—the endognaths of the old Eurypterids.

The next pair of muscles is the pair of anterior dorso-plastron muscles (63). This muscle pair evidently belongs to a segment posterior to the segments represented by the group already discussed, and belongs, therefore, in all probability to the same segment as the sixth pair of prosomatic appendages,—the ectognaths of the old Eurypterids. This can be settled by the nerve supply

<sup>1</sup> "On the Structure of the Mouth and Pharynx of the Scorpion," by T. Huxley, *Q. J. Micr. Sci.*, vol. viii., 1860, p. 250.

or the embryological development. In the Eurypteridæ it seems most highly probable that the dorso-ventral muscles of each half of the segments belonging to the endognaths should be compressed together and separate from the dorso-ventral muscle belonging to the ectognathal segment, on account of the evident concentration and small size of the endognathal segments in contradistinction to the separateness and large size of the ectognathal segment.

The striking peculiarity of this muscle pair, which distinguishes it from all other muscles in the scorpion, is the common attachment of the muscles of the two sides in the mid-dorsal line, so that the pair of muscles forms an arch through which the alimentary canal and dorsal vessel pass.

The same dorso-ventral muscles are present in *Phrynos*, and in this animal the fibres of this pair of muscles (63) actually interlace before their attachment to the prosomatic carapace, so that the attachment of the muscle on each side overpasses the mid-dorsal line, and a true crossing occurs. In fig. 5 the position of this pair of muscles is shown just posterior to the brain mass. This muscle I will call the oblique muscle.

Finally we come to the muscles (64) and (65), the median and posterior dorso-plastron muscles, which run close together. Both muscles are attached to the plastron, and, therefore, to that extent belong to the prosomatic region; they are attached dorsally close to the junction of the prosoma and mesosoma. This position of the first mesosomatic dorso-ventral muscle belonging to the opercular segment may be compared with the position of the first mesosomatic dorso-ventral muscle in *Limulus* which has become attached to the prosomatic carapace; in both cases we see an indication that the foremost mesosomatic dorso-ventral somatic muscles tend to take up a prosomatic position.

As to the pair of small muscles (64), I should imagine that they represent the dorso-ventral muscles of the seventh prosomatic segment (if the pair of muscles (63) belong to the segment of the sixth locomotor prosomatic appendage), i.e., they belong to the chilarial segment or metastoma.

I desire to draw especial attention to the fact that the dorso-ventral muscle (64), which represents the seventh segment, always runs close alongside the dorso-ventral muscle (65), which

represents the first mesosomatic or opercular segment. The significance of this fact will appear when I deal with Miss Platt's and Neal's observations.

I have dwelt thus far on these muscles of the scorpion and *Limulus* because the muscular arrangements of the old sea scorpions must have been fashioned after those of both *Limulus* and *Scorpion*, and these observations of Benham and Miss Beck are the only full reliable description of such musculature as far as I am aware. I want especially to draw attention to the nature of this musculature because of the importance of the formation of muscle segments in estimating the segmentation of the vertebrate head, and especially in estimating the meaning of the eye-muscles.

*Evidence of Segmentation given by the Cœlomic Head Cavities.*

In the head region of the vertebrate, morphologists depend largely for the estimation of the number of segments upon the embryonic divisions of the mesoderm, and, therefore, upon the number of cœlomic cavities in this region, the walls of which give origin to the striated muscles of the head, so that the question of the number of segments depends very largely upon the origin of the muscles from the walls of these head cavities. It is therefore interesting to examine whether a similar criterion of segmentation holds good in such a segmented animal as *Limulus*, or in the members of the scorpion group, in which the number of segments are known definitely by the presence of the appendages. In *Limulus* we know from the observations of Kishinouye<sup>1</sup> that a series of cœlomic cavities are formed embryologically in the various segments of the mesosoma and prosoma, in a manner exceedingly similar to their formation in the head region of the vertebrate, and he has shown that in the *mesosoma* a separate cœlomic cavity exists for each segment, so that just as the dorso-ventral somatic muscles are regularly segmentally arranged in this region, so are the cœlomic cavities, and we should rightly judge of the number of segments in this region by the consideration of the correspondence of these cavities with the mesosomatic appendages. Similarly, in the vertebrate we find every reason to believe that a single, separate head cavity corresponds to each of the branchial segments in the

<sup>1</sup> *Op. cit.*

opisthotic region, and therefore we should rightly judge of the number of segments by the division of the mesoderm in this region.

In the prosomatic region of *Limulus*, we have seen that the dorso-ventral muscles are not arranged with such absolute segmental regularity as in the mesosomatic region, and Kishinouye's observations show that the coelomic cavities in this region do not correspond absolutely with the number of prosomatic appendages. His words are:<sup>1</sup>—

A pair of coelomic cavities appear in every segment except the segments of the 2nd, 3rd, and 4th appendages, in which the coelomic cavity does not appear at all. At least eleven pairs of these cavities are produced. The eleventh pair belongs to the seventh abdominal segment.

The first pair of coelomic cavities is common to the cephalic lobe and the segment of the first appendage (*i.e.*, the chelicerae).

The second coelomic cavity belongs to the segment of the fifth appendage. It is well developed.

The ventral portion of the second coelomic cavity remains as the coxal gland.

Consequently, if we were to estimate the number of segments in this region by the number of coelomic cavities, we should not judge rightly, for we should find only four cavities and seven appendages, as is seen in the following table:—

| LIMULUS.     |                                  |                          |                    |                    | VERTEBRATE. |
|--------------|----------------------------------|--------------------------|--------------------|--------------------|-------------|
| Segments.    | Appendages.                      | (Eurypterid Appendages.) | Coelomic Cavities. | Coelomic Cavities. |             |
| Prosomatic.  | 1 { Chelicerae or 1st locomotor. | } Chelicerae.            | 1                  | Anterior.          |             |
|              | 2 2nd locomotor.                 |                          |                    |                    |             |
|              | 3 3rd do.                        | } Endognatha.            | 2                  | Premandibular.     |             |
|              | 4 4th do.                        |                          |                    |                    |             |
|              | 5 5th do.                        |                          |                    |                    |             |
|              | 6 6th do.                        | Ectognath.               | 3                  | } Mandibular.      |             |
|              | 7 Chilaria.                      | Metastoma.               | 4                  |                    |             |
| Mesosomatic. | 8 Operculum.                     | } Operculum { Genital.   | 5                  | } Hyoid.           |             |
|              | 9 1st branchial.                 |                          | 6                  |                    |             |
|              | 10 2nd do.                       | 2nd branchial.           | 7                  | 1st branchial.     |             |
|              | 11 3rd do.                       | 3rd do.                  | 8                  | 2nd do.            |             |
|              | 12 4th do.                       | 4th do.                  | 9                  | 3rd do.            |             |
|              | 13 5th do.                       | 5th do.                  | 10                 | 4th do.            |             |
|              | 14 6th do.                       | ...                      | 11                 | ...                |             |

<sup>1</sup> *Op. cit.*, p. 81.

The second cavity would in reality represent four segments belonging to the 2nd, 3rd, 4th, 5th locomotor appendages, *i.e.*, the very four segments which in the Eurypterids are concentrated together to form the endognaths, and we should be justified in putting this interpretation on it, because, according to Kishinouye, its ventral portion forms the coxal gland, and according to Lankester<sup>1</sup> the coxal gland sends prolongations into the coxa of the 2nd, 3rd, 4th, 5th locomotor appendages. Similarly, in the vertebrate we find three head cavities in the region which corresponds, on my theory, to the prosomatic region of *Limulus*, (1) the anterior cavity of Miss Platt, (2) the premandibular cavity, and (3) the mandibular cavity, which, if they corresponded with the prosomatic coelomic cavities of *Limulus*, would represent not three segments but seven segments, as follows:—the anterior cavity of Miss Platt would correspond to the first coelomic cavity, *i.e.*, the cavity of the cheliceræ segments in both *Limulus* and the Eurypterids; the premandibular, to the second coelomic cavity, representing, therefore, the 2nd, 3rd, 4th, 5th prosomatic segments in *Limulus* and the endognathal segments in the Eurypteridæ; and the mandibular, to the 3rd and 4th coelomic cavities, representing the last locomotor and chilarial segments in *Limulus*, *i.e.*, the ectognathal and metastomal segments in the Eurypteridæ.

It is worthy of note that, in respect to its coelomic cavity as in its position and origin in the central nervous system, the first pair of appendages, the cheliceræ, retain a unique position, differing from the rest of the prosomatic appendages.

In the table, I have shown how the vertebrate coelomic cavities may be compared with those of *Limulus*; and I now proceed to consider the evidence obtained by morphologists and anatomists as to the number of segments supplied by the trigeminal nerve group.

#### *The Segments belonging to the Trigeminal Nerve Group.*

We see from this sketch that the test whether the trigeminal group of nerves of the vertebrate have been derived from the

<sup>1</sup> "On the Skeleto-trophic Tissues and Coxal Glands of *Limulus*, *Scorpio*, and *Mygale*," *Q. J. Micr. Sci.*, p. 129, vol. xxiv., 1884.



prosomatic group of nerves of the invertebrate would be afforded by the answer to the following morphological and anatomical questions:—

1. Do we find in the vertebrate two segmentations in this region corresponding to the two segmentations in the branchial region, *i.e.*, a somatic or dorsal series of segments and a splanchnic or ventral series of segments? These latter would not be branchial, but rather of the nature of free tactile appendages; so that it is useless to look for or talk about gill slits, although such appendages, being serially homologous with the branchial mesosomatic appendages, would readily give rise to the conception of branchial segments.

2. Is there morphological evidence that the trigeminal nerve is not the nerve belonging to a single segment, or even to two segments, but is really a concentration of at least six, probably seven, segmental nerves?

3. Is there morphological evidence that the oculomotor and trochlearis nerves which on all sides are agreed to belong to the trigeminal segments, are not single nerves belonging each to a single segment, but the somatic motor roots belonging to the same segments as those to which the trigeminal supplies the splanchnic roots?

4. If so, then also the mesoderm segments which give origin to the eye-muscles, and therefore the head cavities of this region, ought to correspond with the trigeminal segments, although it is likely enough, considering the concentration of parts in this region, and the difficulty already present of the want of numerical agreement between the prosomatic appendages and the prosomatic coelomic cavities in *Limulus*, that the actual number may be difficult to decide.

5. Is there anatomical evidence that the ganglion of origin of the motor Vth is not a single ganglion, but a representative of many, probably seven?

6. Is there anatomical evidence that the ganglia of origin of the oculomotor and trochlearis nerves represent many ganglia, probably seven?

7. Is there any evidence that the organs originally supplied by the motor part of the trigeminal nerve are directly comparable with prosomatic appendages?

*Morphological Evidence of the Number of Segments belonging to the Trigeminal Nerve.*

I will first consider the first four of these questions, *i.e.*, the morphological evidence. The question of the nature and number of these most anterior head segments is by no means settled by morphologists; it is only possible to indicate the opinion held by those who have chiefly been engaged in this investigation.

The basis upon which the present-day opinion rests is v. Wijhe's researches, which have led to the conclusion that this foremost region, just as the hindmost region, was originally composed of segments marked out by divisions of the mesoblast, each of which contained a coelomic cavity, and was separable into two parts, dorsal and ventral. From the dorsal parts or somites arose the muscles supplied by the oculomotor and trochlearis nerves, from the ventral parts or lateral plates the muscles supplied by the trigeminal; in accordance, therefore, with the more hindmost segments, and because the unit of measurement was the branchial pouch, *i.e.*, a paired diverticulum of the gut, it was assumed that the ventral parts of these mesoblastic segments originally formed the walls of a series of visceral or branchial pouches, and thus the conception arose that the whole head end of the body has been formed by the modification of a series of branchial pouches comparable with those in the opisthotic region. Such a conception, which has especially been put forward by Marshall, even to making the 1st or olfactory nerve a branchial nerve, and Dohrn, is remarkably strange when one sees that throughout the animal kingdom there is no evidence of *all* the foremost segments of the animal being told off for respiration purposes.

This supposition that the trigeminal nerve belonged originally to a series of branchial pouches in the same way as the vagus and glossopharyngeal was largely due to the habit of looking at the cranial nerves as divisible into two great groups, respectively in front of and behind the auditory capsule, *i.e.*, pro-otic and opisthotic, of which the former included the trigeminal and facial and the latter the glossopharyngeal and vagus nerves. In this

foremost group, as so defined, which was looked upon as a natural group, distinct evidence of visceral and branchial pouches were seen in connection, namely, with the facial nerve, and it was therefore imagined that the rest of the members of this group, viz., the segments in connection with the trigeminal nerve also were originally built up in a similar manner.

In my opinion, as already stated in Part IV. of this series of papers, the segments supplied by the facial are clearly in *Ammocoetes* the foremost of the respiratory segments, and ought therefore to be classed with the rest of the opisthotic segments, and not with the pro-otic; the close relationship and confusion between the Vth and VIIth in the vertebrates is to my mind explainable, as will appear in the sequel, as a consequence of the amalgamation of the last prosomatic and first mesosomatic appendages. In front of the region of the facial nerve there is no evidence of any visceral or branchial pouches. The morphological evidence, then, of segments in the region of the trigeminal has not been proved to be due to the presence of branchial pouches, but to the divisions of the mesoderm; and coming now to the question of the number of segments belonging to this region, we see that v. Wijhe considered there were two only, of which the ventral mesoderm segments formed the splanchnic muscles supplied by the trigeminal, while the two dorsal segments formed the somatic muscles supplied by the oculomotor and trochlearis nerves respectively; the segmental coelomic cavities belonging to these two segments being the premandibular and mandibular respectively.

Of these two segments the muscles of mastication arose from the ventral part of the second or mandibular, the splanchnic muscles belonging to the premandibular not being definable. Since v. Wijhe many papers have appeared, all in the direction of increasing the number of segments belonging to this region. Thus, especially Miss Platt,<sup>1</sup> who has been confirmed by Hoffmann<sup>2</sup> and Neal,<sup>3</sup> finds in *Acanthias vulgaris* a cavity in front

<sup>1</sup> J. B. Platt, "A Contribution to the Morphology of the Vertebrate Head, based on a study of *Acanthias vulgaris*," *Journ. Morph.*, vol. v. p. 79.

<sup>2</sup> C. K. Hoffmann, "Zur Entwicklungsgeschichte des Selachier Kopfes," *Anat. Anz.*, Bd. 9, p. 638.

<sup>3</sup> H. V. Neal, "The Segmentation of the Nervous System in *Squalus Acanthias*," vol. xxxi. n. 7, *Bull. of Mus. of Comp. Zool.*, Harvard, 1898.

of the premandibular, to which she has given the name of the anterior cavity, so that there are three coelomic cavities, not two, viz., (1) anterior cavity, (2) premandibular, and (3) mandibular. She finds that the anterior cavity forms a muscle which comes to nothing, while the premandibular forms in its dorsal part four muscles—superior rectus, inferior rectus, internal rectus, and inferior oblique; further, the mandibular is double, forming in the dorsal part of its one portion the superior oblique muscle, in the other a muscle called by her the mandibular muscle, which comes to nothing. In a footnote, *op. cit.*, p. 199, Neal states that he considers Miss Platt's evidence of two segments in the mandibular cavity to be illusory. Miss Platt therefore considers that the trigeminal corresponds to four segments, viz., (1) anterior, (2) premandibular, and (3) and (4) mandibular, while corresponding to these segments we have dorsally seven muscles formed, viz., (1) anterior, muscle lost; (2), (3), (4), (5) premandibular, muscles supplied by IIIrd nerve, viz., superior rectus, inferior rectus, internal rectus, and inferior oblique; (6) mandibular, muscle supplied by IVth nerve, viz., superior oblique; (7) mandibular, muscle lost. If, then, as seems most probable, these four divisions of the premandibular be looked upon as four different segments fused into one, we should have seven dorsal segments belonging to this region, just as is asserted to be the case in *Torpedo* by Dohrn.<sup>1</sup> Dohrn's mesoderm segments have been observed by Platt to a certain extent, but are not considered by her to have segmental value, because they are not uniform on the two sides. At the same time, if the premandibular cavity was really a fusion of four separate cavities belonging respectively to the four eye-muscles supplied by the oculomotor nerve, then there would be no discrepancy in number between Dohrn and Miss Platt. Dohrn himself does not seem to me to lay any great stress on the absolute number of segments belonging to these different cavities respectively, but rather desires to emphasise strongly that the oculomotor and abducens nerves are each not single segmental nerves, but multiple nerves, and that the premandibular cavity is not a single head cavity, but a

<sup>1</sup> A. Dohrn, "Neue Grundlagen zur Beurtheilung der Metamerie des Kopfes," *Mitth. Zool. Stat. Neapel*, Bd. 9, p. 330, 1890.

fusion of many such cavities. Further, we must, I think, agree with Dohrn that if there are a number of dorsal segments corresponding to the oculomotor and trochlearis, there must have been a similar number of ventral segments corresponding to the motor part of the trigeminal, even though the corresponding splanchnic muscles have only been discovered for the last two or mandibular segments, and not for the premandibular and anterior segments.

I would then suggest that the morphological evidence of muscle segments is compatible with the conclusion that the primitive animal possessed seven segments in this region, each of which originally consisted of a somatic part and a splanchnic part, or, to use the language of these papers, prosomatic segments, each composed of a body part and an appendage, and that these seven prosomatic segments originally each contained a coelomic cavity, but these coelomic cavities became fused in such a way as to form (1) an anterior head cavity belonging to the first segment, (2) a premandibular belonging to the next four segments, and (3) a mandibular belonging to the last two prosomatic segments. Surely such a teaching of embryology is most striking when we see, as already mentioned (p. 483), how the coelomic cavities are arranged in *Limulus*.

So far the segmental value has been considered from the motor side, it has also been largely discussed from the sensory side, the question here being not so much the distribution of the sensory nerves as the number of ganglia belonging to each of the cranial nerves.

With respect to this question, morphologists have come to the conclusion that there is a marked difference between spinal and cranial nerves, in that whereas the posterior root ganglia of the spinal nerves arise from the central nervous system itself, *i.e.*, from the neural crest, the ganglia of the cranial nerves arise partly from the neural crest, partly from the proliferation of cells on the surface of the animal; and because of the situation of these proliferating epidermal patches over the gill clefts in the case of the vagus and glossopharyngeal nerves, they have been called by Froriep<sup>1</sup> and Beard<sup>2</sup> branchial sense organs.

<sup>1</sup> Froriep, *Archiv f. Anat. u. Physiol., Anat. Abth.*, 1888, pp. 1-55.

<sup>2</sup> Beard, *Quart. Journ. Micr. Sci.*, vol. 26, p. 95, 1885.

Beard divides the cranial ganglia into two sets, one connected with the neural ridges, called the neural ganglia, and the other connected with the surface cells, which he calls the lateral ganglia. This second set corresponds to Kupffer's epibranchial ganglia. Now it is clear that in the case of the vagus nerve, where, as is well shown in *Ammocoetes*, the nerve is not a single segmental nerve, but in reality is made up of a number of nerves going to separate branchial segments, the indication of such segments is not given by the main vagus ganglion or neural ganglion, but by the series of lateral ganglia. So also it is argued in the case of the trigeminal, if in addition to the ganglion cells arising from the neural crest separate ganglion masses are found in the course of development in connection with proliferating patches of the surface (plakodes, Kupffer calls them), then such isolated lateral ganglia are indications of separate segments, just as in the case of the vagus, even though the separate segments do not show themselves in the adult. So far the argument appears to me just, but the further conclusion that the presence of such plakodes shows the previous existence of *branchial* sense organs, and therefore that such ganglia are *epibranchial* ganglia, indicating the position of a lost gill slit, is not justified by the premises; if, as I suppose, the trigeminal nerve supplied a series of non-branchial appendages serially homologous with the branchial appendages supplied by the vagus, then it is likely enough that the trigeminal should behave with respect to its sensory ganglia similarly to the vagus nerve, without having anything to do with branchiæ.

I prefer, therefore, Beard's original term 'lateral ganglia' to a term like Kupffer's 'epibranchial ganglia,' which prejudices the question. Even 'lateral' implies, in the sense in which Beard used it, a connection with the series of sense organs of the lateral line, so that I should prefer a colourless term like 'plakodal' to express this series of ganglia.

Such plakodal ganglia, then, may give valuable indication of non-branchial segments as well as branchial ones. The researches of Kupffer<sup>1</sup> on the formation of the trigeminal ganglia in *Ammocoetes* are the chief attempt to find out from the side of

<sup>1</sup> "Die Entwicklung der Kopfnerven von *Ammocoetes Planeri*," München, 1895.

the sensory ganglia the number of segments originally belonging to the trigeminal. In the full-grown *Ammocoetes*, as is well known, there are two distinct ganglia belonging to the trigeminal, the one the ganglion of the *ram. ophthalmicus*, the other the main ganglion.

These two ganglia arise, according to Kupffer, as follows:— From the neural crest, *i.e.*, from the *Zwischenstrang*, two ganglionic masses arise, each of which becomes connected with a proliferating patch of skin, forming altogether two chief ganglia; the part of the ganglion derived from the skin, the lateral ganglion, is histologically distinct, being more cellular, from the part derived from the central nervous system, the median ganglion, which is more fibrous, so that Kupffer's chief ganglion represents Beard's neural ganglion in its median part only. In addition to this connection with the skin, other connections are made later, to which he ascribes the formation of a series of epibranchial ganglia belonging to the trigeminal group. Some of these so-called epibranchial ganglia arise so closely in connection with the lateral part of the chief ganglion as to make it appear decidedly arbitrary to separate such lateral ganglia into a different category to the epibranchial. His epibranchial ganglia are derived, one in connection with the second chief ganglion, and four in connection with a separate nerve root, which does not possess a chief ganglion, to which he gives the name of *n. abducens*; these four epibranchial ganglia are arranged in a row, and the foremost is said to form the lens. Afterwards these epibranchial ganglia become absorbed into the two main ganglia, or disappear.

I do not understand that he himself has traced the so-called *n. abducens* into the external rectus muscle, but that he relies on Ahlborn's description. Both he and Ahlborn consider that this nerve arises from the foremost part of the motor trigeminal nucleus, and therefore is not homologous with the *n. abducens* of higher vertebrates.

It seems clear that further research is necessary to establish the true position of this nerve root.

In any case Kupffer's investigations point to a multiple of segments supplied by the trigeminal group, and he himself concludes that the trigeminal originally supplied five at least, prob-



ably six, segments. For my own part, if we take the lateral or plakodal ganglia as indicative of segments, then Kupffer's evidence points to seven rather than five segments; for in addition to his five plakodal ganglia, to which he gives the name epi-branchial ganglia, he describes a lateral ganglion which is equally plakodal, as forming a part of each chief ganglion, so that he describes seven plakodal ganglia as belonging to the trigeminal, rather than five.

I have thought it worth while to state thus briefly Kupffer's results, not because their meaning is clear and devoid of dispute, but as indicating that on the sensory side as well as on the motor side the tendency of the present day is to show that the trigeminal represents a multiple of nerves. Whatever the ultimate verdict on Kupffer's work may be, it is clear and suggestive that the ganglion formation in the case of the cranial nerves differs from that of the spinal nerves in that the formation of some of the cells of the former has special relation to special skin patches, while such a relation is not found in the formation of the latter; a more primitive, more ancestral method of formation, according to my view, and one associated with the former presence of appendages, for it is in the appendage region only that such plakodal ganglia are formed.

In accordance with the views of this series of papers, a possible interpretation of Kupffer's plakodal ganglia would be given as follows:—

Beard,<sup>1</sup> who after Froriep drew attention to this relation of the cranial ganglia to special skin patches, has compared them with the parapodial ganglia of Annelids, *i.e.*, ganglia in connection with Annelidan appendages; whether we are here obtaining a glimpse of the far off Annelidan ancestry of both Arthropods and Vertebrates it would be premature at present to say; it is natural enough to expect, on my view, to find evidence of Annelidan ancestry in Vertebrate embryology (as has been so often asserted to be the case), seeing that undoubtedly the Arthropoda are an advanced stage of Annelida; and indeed the way is not far when we consider Beecher's<sup>2</sup> evidence that the Trilobites

<sup>1</sup> "The Development of the Peripheral Nervous System in Vertebrates," *Amer. Jour. of Micr. Sci.*, 1888.

<sup>2</sup> Beecher, "Natural Classification of the Trilobites," *Amer. Jour. of Sci.*, Ser. 4, vol. iii., 1897.



belong to the Phyllopoda, certainly a primitive Crustacean group, which Bernard<sup>1</sup> derives directly from the Chætopoda.

The foremost ganglion on each side—ganglion ophthalmicum—consists of a chief ganglion and a lateral ganglion, thus indicating a single most anterior pair of appendages, possibly the chelicerae.

Then comes the so-called n. abducens, with four epibranchial ganglia and no chief ganglion, indicating on each side four appendages close together, possibly the endognaths.

Then finally, on each side, the second large ganglion, with one lateral and one epibranchial ganglion, indicating two pairs of appendages, the ectognaths and the metastoma.

*Anatomical Evidence of the number of Segments belonging to the Trigeminal Nerve.*

If we turn now to the work of the anatomists, and endeavour to get a clue to the past history of the motor part of the trigeminal by the consideration of its origin in the central nervous system, we see that its centre of origin is exceedingly striking in its distribution; we may take it for granted that a nucleus of cells giving origin to one or more segmental motor nerves will possess a greater or less longitudinal extension in the central nervous system, according to the number of fused separate segmental centres it represents. Thus a nucleus like that of the IVth nerve or of the facial is small and compact in comparison to the long extending conjoint nucleus of the vagus and cranial accessory.

Upon examination of the motor nucleus of the trigeminal, we find at first sight a compact or well-defined nucleus, the *nucl. masticatorius*, the nerves of which supply the masseter, temporal, and other muscles, so that the anatomical evidence at first sight appears to bear out V. Wijhe's conclusion that the motor trigeminal supplies at most two segments; further examination, however, shows that this is not all, for the extraordinary so-called descending root of the Vth must be taken into consideration in any question of the origin of the motor elements, just as the equally striking ascending root enters

<sup>1</sup> Bernard, "The Apodidæ; A Morphological Study," *Nature Series*, 1892.

into the consideration of the meaning of the sensory elements of the Vth.

The question of course arises, what is this descending root of the Vth—is it motor or sensory? and the answer is distinctly in favour of its being motor.

In a paper by Gehuchten<sup>1</sup> a history is given, and it is stated that Deiters originally thought this descending root belonged to the IVth nerve, and lately Golgi, by means of his silver method, has asserted the same thing. Duval, however, has shown this to be erroneous in the case of the mole, where the IVth nerve is atrophied, and yet these cells and nerves exist. Kölliker states that they undoubtedly belong to the Vth nerve, and form a motor root, because of the thickness of the fibres, their direct connection with the portio minor, and the impossibility of any other explanation. Lugaro has shown by Golgi's method that the axis-cylinder processes of these vesicular cells form the descending root of the trigeminal; and Gehuchten, by Golgi's method, has traced in the trout the axis-cylinder processes of these cells into the motor root of the trigeminal. Also Mayser, in teleosteans, carp, etc., finds what he believes to correspond to the cells of the descending root of mammals, in the shape of vesicular cells which start in the neighbourhood of the posterior commissure, are arranged in groups of 2-6, and are, he believes, though this he has not been able to prove satisfactorily, connected by means of large fibres with that part of the motor root of the trigeminal which arises from the anterior nucleus; in the fish the main motor nucleus is double, being divided into an anterior and a posterior nucleus. Finally Obersteiner, in his well-known anatomy of the central nervous system, says:—

“The motor fibres of the trigeminal are supposed to arise from three sources:<sup>2</sup>

“1. The motor nucleus (*nucl. masticatorius*).

“2. From the cells of the *Locus cœruleus* by way of the posterior longitudinal bundle to the motor root.

“3. From the region of the mid-brain the motor root receives an important addition of thick fibres, which form the cerebral

<sup>1</sup> Gehuchten, “De l'origine du pathétique et de la racine supérieure du trijumeau,” *Acad. d. Sci. Belg. Bulletin*, 3rd ser., vol. 29, 1895.

<sup>2</sup> *Nervösen Centralorgane*, 1896, 3<sup>te</sup> Aufl., page 404.

or descending root. The large round vesicular cells from which the fibres of the descending root arise form no single compact group, but are partly single, partly arranged like little bunches of grapes, as far as the region of the anterior corpora quadrigemina. The further we go brainwards the smaller is the number of fibres. In the region of the anterior corpora quadrigemina, the few cells of origin are found more and more median; so that the uppermost trigeminal fibres descend in curves almost from the mid-line, as is shown by the exceptional occurrence of one or more of the characteristic cells above the aqueduct. At the height of the posterior commissure one finds the last of these trigeminal cells."

Obersteiner considers that the origin of the motor root from (1) and (3) is certain, but from (2) is doubtful.

The most recent attempt to settle the meaning of the descending root of the Vth nerve is a paper by Terterjanz,<sup>1</sup> in which he attempts experimentally to test Kölliker's suggestion that the muscles supplied by the descending root may be the *tensor veli palatini* and the *tensor tympani*. As a consequence of the extirpation of the *tensor veli palatini* in young kittens, he finds 20–38 days afterwards distinct degeneration in the fibres of the descending root on both sides, as given by the Marchi method, and concludes that Kölliker's suggestion is a good one, and that the *m. tensor veli palatini* is one of the muscles innervated by the descending root of the Vth nerve.

The anatomy of the Vth nerve reveals, then, three most striking facts:—

1. The motor nucleus of the Vth extends from the very commencement of the infra-infundibular region to nearly the commencement of the nucleus of the VIIth; in other words, the motor nucleus of the Vth extends through the whole prosomatic region, just as it must have done originally if its motor nerves supplied the muscles of the prosomatic appendages. Such an extended range of origin is indicative of the remains of an equally extended series of segmental centres or ganglia.

2. Of these centres the caudalmost have alone remained large and vigorous, constituting the *nucleus masticatorius*, which in the fish is divided into an anterior and posterior group, thus

<sup>1</sup> "Die obere Trigemini-Wurzel," *Arch. f. mikr. Anat.*, Bd. liii. s. 632, 1899.

indicating a double rather than a single nucleus; while the foremost ones have dwindled away until they are represented only by the cells of the descending root, the muscles of these segments being still represented by possibly the *tensor veli palatini* and the other muscles innervated from these cells.

3. The headmost of these cells takes up actually a position dorso-lateral to the central canal, so that the groups on each side nearly come together in the mid-dorsal line; a very unique and extraordinary position for a motor cell group, but not unlikely when we recall to mind Brauer's<sup>1</sup> assertion as to the shifting of the foremost prosomatic ganglion cells of the scorpion from the ventral to the dorsal side of the alimentary canal.

The anatomical evidence seems to me to bear out the morphological evidence, and suggests distinctly that the prosomatic region of the brain gave origin to a series of nerves, the trigeminal nerves, which supplied a series of prosomatic appendages, probably seven, the foremost of which, probably five, dwindled away and became insignificant, leaving as trace of their former presence the descending root of the Vth, while the hindmost, probably two, remained vigorous and developed, leaving as proof of their presence the *nucleus masticatorius*. The evidence as to the truth of this suggestion and the exact nature of this dwindling process will be given when I come to point out the teaching of *Ammocetes*; while the importance of the last two appendages comes clearly to light when we consider the changes which take place at transformation.

#### *The Meaning of the Eye Muscle Nerves.*

So far I have discussed in these series of papers the meaning of the various segmental cranial nerves, *i.e.*, infra-infundibular nerves supplying splanchnic segments, and have come to the conclusion that they were all derived from nerves to mesosomatic and prosomatic appendages. I have, however, as yet not discussed the corresponding nerves to somatic segments, except incidentally. In the case of the trigeminal group, it is impossible to discuss the splanchnic segments without taking into consideration at the same time the somatic segments, *i.e.*, the

<sup>1</sup> *Loc. cit.*

nerves of the prosoma itself, so that at this stage of the argument it is advisable to consider the innervation of the segments of the mesosoma and prosoma. Here also it is advisable to consider first the motor elements, in other words the nerves which supply the musculature derived from the dorsal mesoblastic segments of v. Wijhe; and in order to simplify the task, I will take, in the first place, all the segments up to and inclusive of the glossopharyngeal, because, as already mentioned, that is a more fixed point than the vagus, which, as is known, is variable in the number of its segments, and also in order not to confuse the issue by the discussion of the position of the hypoglossal nerve. The only universally recognised somatic nerves belonging to these segments which exist in the adult are the nerves to the eye-muscles, of which, according to v. Wijhe, the oculomotor is the nerve of the 1st segment; the trochlearis of the 2nd, and the abducens of the 3rd, while the nerves and muscles belonging to the 4th and 5th segments, *i.e.*, the 2nd facial and glossopharyngeal segments respectively, show only the merest rudiments, and do not exist in the adult. One significant fact appears in this statement of v. Wijhe, and is accepted by all those who follow him, *viz.*, that the oculomotor nerve has equal segmental value with the trochlearis and the abducens, although it supplies a number of muscles, each of which, on the face of it, has the same anatomical value as the superior oblique or external rectus. Dohrn alone, as far as I know, as already pointed out, insists upon the multiple character of the oculomotor nerve.

As far as the anatomist is concerned, the evidence is becoming clearer and clearer that the nucleus of the 3rd nerve is a composite ganglion composed of a number of nuclei similar to that of the trochlearis, so that if the trochlearis nucleus is a segmental motor nucleus, then the oculomotor nucleus is a combined nucleus belonging to at least four segmental nerves, each of which has the same value as that of the trochlearis.

The investigations of a number of anatomists, among whom may be mentioned Gudden, Obersteiner, Edinger, Kölliker, Gehuchten, all lead directly to the conclusion that this oculomotor nucleus is composed of a number of separate nuclei, some of which, the most anterior and the Edinger Westphal nucleus, contain small

cells, while the others contain large cells. Thus Edinger divides the origin of the oculomotor nerve into a small celled anterior part and a larger posterior part of which the cells are larger and distinctly arranged in three groups—1. dorsal, 2. ventral, and 3. median. Between the anterior and posterior groups lies the Edinger-Westphal nucleus, which is small celled; naturally, the large celled group is that which gives origin to the motor nerves of the eye-muscles, the small celled being possibly concerned with the motor nerves of the pupillary and ciliary muscles. I may mention that Kölliker considers that the anterior lateral nucleus has nothing to do with the oculomotor nerve, but is a group of cells in which the fibres of the post-longitudinal bundle and of the deep part of the posterior commissure terminate.

These conclusions of Edinger are the outcome of work done in his laboratory by Perlia,<sup>1</sup> who says that in new-born animals the nucleus of origin is made up of a number of groups quite distinct from each other, each group being of the same character as that of the trochlearis. He finds the same arrangement in various mammals and birds. Further, he finds that some of the fibres arise from the nucleus of the opposite side, thus crossing as in the trochlearis; these crossing fibres belong to the most posterior of the dorsal group of nuclei, *i.e.*, to the inferior oblique.

The evidence therefore points to the conclusion that the oculomotor nucleus is a multiple nucleus, each part of which gives origin to one of the nerves of one of the eye-muscles.

Edinger,<sup>2</sup> in his latest edition, says that there is such an array of clinical observations, and of facts derived from post-mortem dissections, that one may venture to designate the portion of the nucleus from which the innervation of each individual ocular muscle comes. He gives Starr's table, the latest of these numerous attempts so happily begun by Pick. According to Starr the nuclei of the individual muscles are arranged from before backward, thus :—

<sup>1</sup> *Arch. f. Ophthalmol.*, vol. 35, 1889, p. 287.

<sup>2</sup> *Anatomy of Central Nervous System in Man and in Vertebrates*, translated by Hall, 1899.

|                     |               |
|---------------------|---------------|
| m. sph. iridis.     | m. ciliaris.  |
| m. levator palpebr. | m. rect. int. |
| m. rect. sup.       | m. rect. inf. |
| obl. inf.           |               |

Further, the evidence of the well-known physiological experiments of Hensen and Völkers that the terminal branches of the oculomotor nerve arise from a series of segments of the nucleus, arranged more or less one behind the other in a longitudinal row, leads them to the conclusion that the nuclei of origin are arranged as follows, proceeding from head to tail :—

|                 |                          |
|-----------------|--------------------------|
| Nearest brain,  | 1. Accommodation nerves. |
|                 | 2. m. sphincter iridis.  |
|                 | 3. m. rectus internus.   |
|                 | 4. m. rectus superior.   |
|                 | 5. m. levator palpebræ.  |
|                 | 6. m. rectus inferior.   |
| Most posterior, | 7. m. obliquus inferior. |

It is instructive to compare this arrangement of Hensen and Völkers with the arrangement of the origin of these muscles from the premandibular cavity as given by Miss Platt.

Thus she states that the most posterior part of the premandibular cavity is cut off, so as to form a separate cavity, resembling, except in position, the anterior cavity; this separate most posterior part gives origin to the inferior oblique muscle; then she goes on to describe how the dorsal wall of the remainder of the premandibular cavity becomes thickened to form posteriorly the rudiment of the inferior rectus, anteriorly the rudiments of the superior and internal recti, a slight depression in the wall of the cavity separating these rudiments. The internal rectus is the more median of the two anterior muscles.

In other words, her evidence points not only to a fusion of somites to form the premandibular cavity, but also to the arrangement of these somites as follows, from head to tail :—(1) internal rectus, (2) superior rectus, (3) inferior rectus, (4) inferior oblique, an order precisely the same as that of Hensen and Völkers, and of Starr.

I conclude, from the agreement between the anatomical,



physiological, and morphological evidence, that the IIIrd and IVth nerves contain the motor somatic nerves belonging to the same segments as the motor trigeminal; in other words, to the prosomatic segments; so that the eye-muscles innervated by III and IV represent segmental muscles belonging to the prosoma; and I conclude that originally there were seven prosomatic segments, the first of which is represented by the anterior cavity of Miss Platt, and does not form any permanent muscles; the next four belong to the premandibular cavity, and the muscles formed are superior rectus, internal rectus, inferior rectus, and inferior oblique; and the last two belong to the mandibular cavity, and the muscles formed are Miss Platt's mandibular muscle and the superior oblique. It is, to say the least of it, a striking coincidence that such an arrangement of the coelomic cavities here should be so closely mimicked by the arrangement in the prosomatic region of *Limulus* as already mentioned; it suggests inevitably that the head cavities of the vertebrate are nothing more than the prosomatic and mesosomatic segmental coelomic cavities, as found in animals like *Limulus*. In the table on p. 483 I have inserted the segments in the vertebrate to compare with the *Limulus* segments.

Before we can come to any conclusion as to the original position of these eye-muscles, it is necessary to consider the Vth nerve and the external rectus muscle. This nerve and this muscle belongs to v. Wijhe's 4th segment, *i.e.*, is the somatic segmental muscle belonging to the same segment as the facial; is, in fact, not a segmental muscle belonging to the prosoma, but to the mesosoma. Further, v. Wijhe's researches, and others agree with them, point to the conclusion that this muscle is the only somatic segmental muscle left in all the mesosomatic segments, with the possible exception of the retractor bulbi; for, as already pointed out, the corresponding muscles for the 5th and 6th segments, *i.e.*, the 2nd facial and glossopharyngeal segments do not persist, but are only indicated in the embryo. Neal<sup>1</sup> comes to the conclusion that the existing abducens is the only root which remains permanent among a whole series of corresponding ventral roots belonging to the opisthotic segments, and further points out that the external rectus was originally an

<sup>1</sup> *Op. cit.*



opisthotic muscle which has taken up a pro-otic position, *i.e.*, translating into the language of *Limulus*, etc., a mesosomatic muscle which has taken up a prosomatic position.

With respect to the external rectus muscle, Miss Platt has shown that the mandibular muscle is formed close alongside the external rectus, so that the two are in close relationship as long as the former exists.

What, then, is the interpretation of these embryological facts? As already mentioned, the eye-muscles in *Ammocoetes* must be considered by themselves; they do not belong in structure or position to the longitudinal somatic muscles innervated by the spinal nerves; their structure is not the same as that of the tubular constrictor branchial muscles, but resembles that structure somewhat; their position is dorso-ventral rather than longitudinal; they may be looked upon as a primitive type of somatic muscle segmentally arranged, the direction of which was dorso-ventral.

Also Anderson, in a research not yet published, has shown, and has given me permission to state, that the time of medullation of the nerves supplying these muscles is much earlier than that of the nerves belonging to the somatic trunk muscles, their medullation taking place at the same time as the motor nerves supplying the striated visceral muscles; and Sherrington has observed that these muscles do not possess muscle spindles, while all somatic trunk muscles do. Both these observations are strong confirmation that the eye-muscles must be classified in a different category to the ordinary trunk somatic muscle group.

Remembering the tripartite division of each segmental nerve group in *Limulus* into (1) dorsal or sensory somatic, (2) appendage nerve, and (3) ventral somatic, I venture to suggest that the three nerves, the oculomotorius, the trochlearis, and the abducens, represent the ventral somatic nerves of the prosoma, and partly also of the mesosoma; nerves, therefore, which may have originally contained sensory fibres, and which still contain the sensory fibres of the eye-muscles themselves, according to Sherrington. According to this suggestion, the eye-muscles are the sole survivors of the segmental dorso-ventral somatic muscles, so characteristic of the group from which I imagine the

vertebrates to have sprung. In the mesosomatic region the dorso-ventral muscles which were retained were those of the appendages, and not of the mesosoma itself, because the presumed ancestor breathed after the fashion of the water-breathing *Limulus*, by means of the dorso-ventral muscles of its branchial appendages, and not after the fashion of the air-breathing scorpion, by means of the dorso-ventral muscles of the mesosoma; the only mesosomatic dorso-ventral muscles which were retained were those of the foremost mesosomatic segment, *i.e.*, those supplied by the VIth nerve, which were preserved owing to their having taken on a prosomatic position and become utilised to assist in the movements of the lateral eyes. The behaviour of the foremost pair of mesosomatic vertical muscles in *Limulus*, as already mentioned, is distinctly suggestive in this respect, and still more so are the corresponding pair of muscles in *Scorpio* (65), according to Miss Beck.

The embryonic history of the muscular formation in the mesosomatic or branchial region, as given by v. Wijhe and Neal, shows that the characteristic of this region is the formation of the branchial musculature from the ventral mesoderm segments, and the non-formation of the somatic musculature from the dorsal mesoderm segments, with the exception of the external rectus muscle.

In the prosomatic region the dorso-ventral muscles which were retained were rather those of the prosoma than of the prosomatic appendages. The evidence of Miss Platt, v. Wijhe, and others leads to the following conclusions.

The foremost prosomatic segment stood separate and apart, being situated most anteriorly; the musculature of this segment does not develop, so that the only evidence of its presence is given by the anterior coelomic cavity. This corresponds, according to my scheme, with the first or anterior coelomic cavity of *Limulus*, and therefore represents, as far as the prosomatic appendages are concerned, the first prosomatic appendage pair, or the chelicerae; the appendage muscles being the muscles of the chelicerae, and the dorso-ventral somatic muscles the pair of dorso-chelicerai sternal muscles (61) in the scorpion. Both these sets of muscles therefore dwindle and disappear in the vertebrate. Then came four segments fused together to form

the premandibular segment, the characteristic of which is the apparent non-formation of the musculature from the ventral mesoderm segment, and the formation of the eye-muscles innervated by the oculomotor nerve from the dorsal mesoderm segments. These four segments have been so fused together that v. Wijhe looked upon them as a single segment, and the premandibular cavity as the cavity of a single segment. They represent, according to my scheme, the segments belonging to the endognaths, *i.e.*, the second, third, fourth, fifth pairs of prosomatic appendages; the premandibular cavity therefore represents the second coelomic cavity in *Limulus*, which, according to Kishinouye, is the sole representative of the coelomic cavities of the second, third, fourth, fifth prosomatic segments; the muscles derived from the ventral mesoderm represent the muscles of these appendages, which therefore dwindle and disappear in the vertebrate, with the possible exception of the muscles innervated by the descending root of the trigeminal; the muscles derived from the dorsal mesoderm, *i.e.*, the eye-muscles supplied by the oculomotor nerve, represent the dorso-ventral somatic muscles of these four segments, muscles which are represented in the scorpion by the recti group of muscles, *i.e.*, the median dorso-preoral entosclerite muscles (62).

Then came two segments, the mandibular, in which muscles are formed both from the ventral and from the dorsal mesoderm segments; from the former the main mass of muscles innervated by the motor root of the trigeminal, from the latter the superior oblique muscle and the mandibular muscle of Miss Platt, of which the former alone survives in the adult condition. These two segments are looked upon as a single segment by v. Wijhe, of which the mandibular cavity is the coelomic cavity. They represent, according to my scheme, the segments belonging to the sixth pair of prosomatic appendages or ectognaths, and the seventh pair, *i.e.*, the chilaria or metastoma.

The first part, then, of the mandibular cavity represents the third coelomic cavity in *Limulus*, and the muscles derived from the ventral mesoderm, in all probability the muscles of the tongue in the lamprey (see Part VII.), which represents the ectognaths or sixth pair of prosomatic appendages, while the muscles derived from the dorsal mesoderm, *i.e.*, the superior

oblique muscles, represent the dorso-ventral somatic muscles of this segment, muscles which are represented in the scorpion group by the pair of anterior dorso-plastron or oblique muscles (63).

The second part of the mandibular cavity represents the 4th coelomic cavity in *Limulus* and the muscles derived from the ventral mesoderm, in all probability the muscles of the lower lip in the lamprey (see Part VII.), which represents the metastoma, while the muscles derived from the dorsal mesoderm, *i.e.*, Miss Platt's pair of mandibular muscles, represent the dorso-ventral somatic muscles of this segment, muscles which are represented in the scorpion group by the pair of median dorso-plastron muscles (64).

In connection with this last pair of muscles we find (as already mentioned, p. 500), that the external rectus in the vertebrate represents the 1st dorso-ventral mesosomatic muscle in the scorpion, *i.e.*, the posterior dorso-plastron muscle (65), and, as already mentioned, that it always lies closely alongside the mandibular muscle, just as in the scorpion group muscle (65) always lies alongside (64).

Now, the external rectus muscle is not the only muscle innervated by the VIth or abducens nerve, for the retractor bulbi is also innervated by this nerve. This latter muscle is not considered in Miss Platt's scheme, and it would therefore be very interesting to know how the retractor bulbi is formed.

The question naturally arises—What explanation can you give by which these dorso-ventral muscles attached on each side of the mid-dorsal line to the prosomatic carapace, became converted into the muscles moving the eyeballs of the two lateral eyes; an explanation which must take into account not only the isolated position of the abducens nerve, but also the extraordinary course of the trochlearis. The natural and straightforward answer to this question appears to me quite satisfactory, and I therefore venture to commend it to my readers.

I have argued the case out to myself as follows:—The lateral eyes must have been originally situated externally to the group of muscles innervated by the oculomotor nerve, for a sheet of muscle representing the superior *internal* and inferior rectus

muscles could only wrap round the internal surface of each lateral eye; *i.e.*, the arrangement of the muscle sheet as in the scorpion, about two median eyes, is in the wrong position, for if those two eyes, which are the main eyes in the scorpion, were to move outwards to become two lateral eyes, then such muscle group would form a superior, *external* and inferior rectus group. The evidence, however, of *Eurypterus* and similar forms is to the effect that the lateral eyes became big and the median eyes insignificant and degenerate. If, then, with the degeneration of the one and the increasing importance of the other, these lateral eyes came near the middle line, then the muscular group (62) which I have called the recti group would naturally be pressed into their service, and would form an internal and not an external group of eye-muscles.

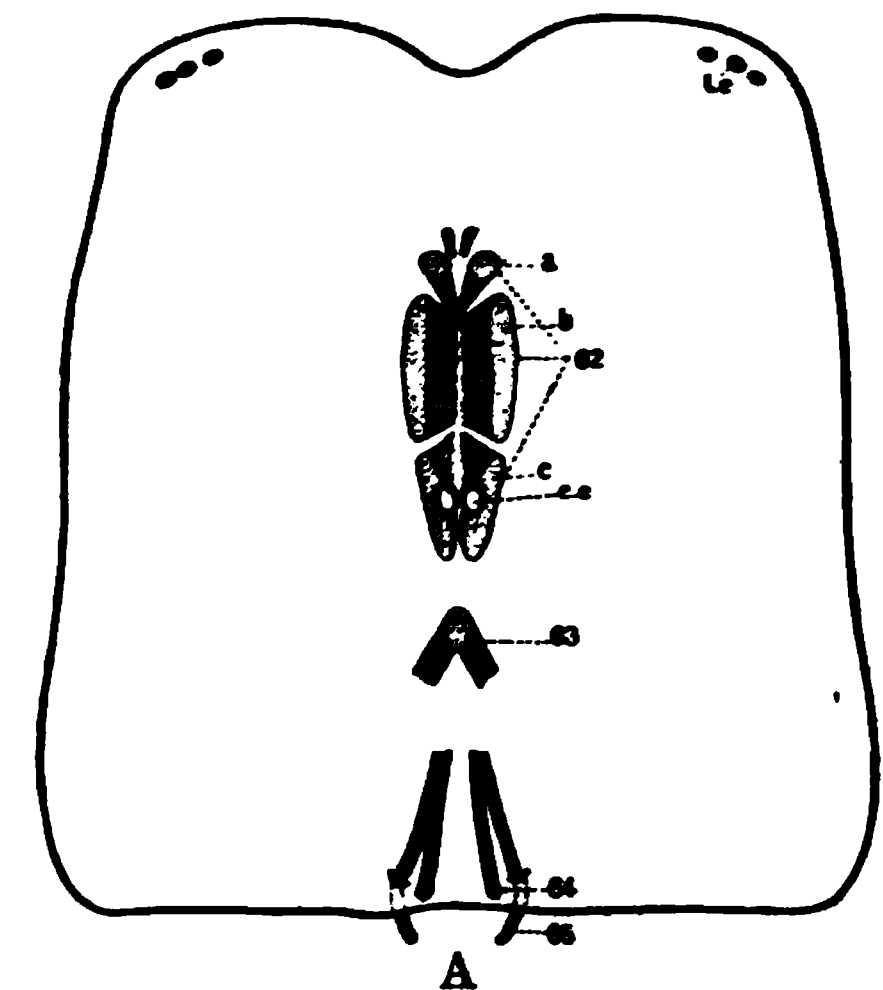
In fig. 8A, taken from Miss Beck's paper, I have shown the relative position of the eyes and the segmental dorso-ventral prosomatic muscles on the carapace of the scorpion. In fig. 8B I have drawn the prosomatic carapace of *Eurypterus Scouleri*, taken from Woodward's paper, with the eyes as represented there; in this I have inserted the segmental dorso-ventral muscles after the fashion of the scorpion, thereby demonstrating how, with the degeneration of the median eyes and the large size of the lateral eyes, the recti muscles of the scorpion would approach the position of an internal recti group to the lateral eyes, and so give origin to the group of muscles innervated by the oculomotor nerve.

In the *Eurypterus* these large eyes are large single eyes, not separate ocelli as in the scorpion.

All, then, that is required is that in the first formed fishes, which still possessed the dorso-ventral muscles of their Eurypterid ancestors, the lateral eyes should be the important organs of sight, large and near the mid-dorsal line.

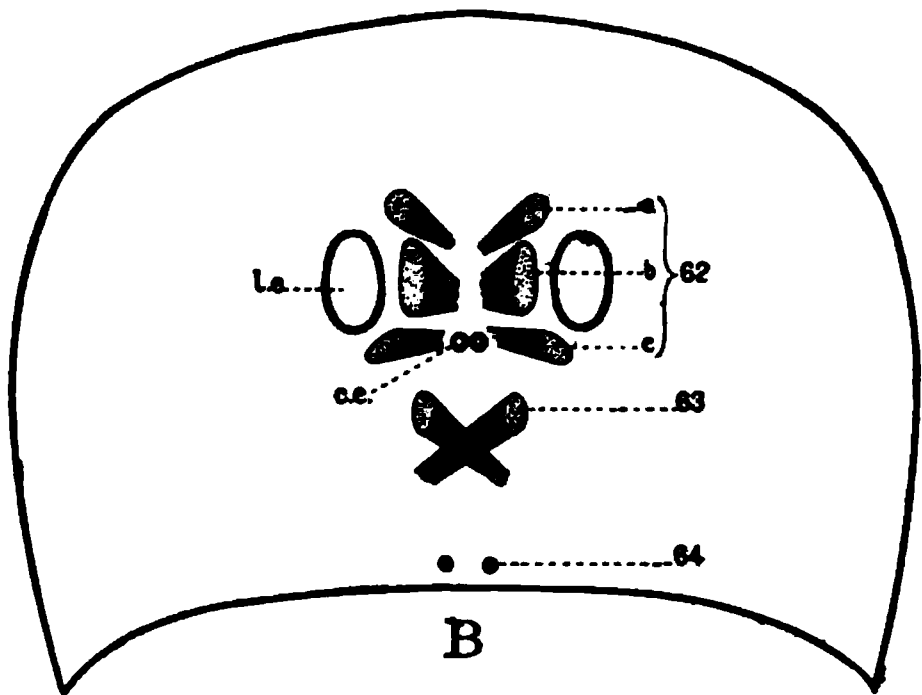
Such indeed is found to be the case. In amongst the masses of Eurypterids found in the upper Silurian deposits at Oesel, as described by Rohon,<sup>1</sup> numbers of the most ancient fish forms are found belonging to the genera *Thyestes* and *Tremataspis*;

<sup>1</sup> "Die obersilurischen Fische von Oesel by J. W. Rohon, 1st Theil Thyestidæ und Tremataspidæ," *Mém. de l'Acad. Imp. d. Sci. d. St Petersburg*, vii. ser., vol. xxxviii., 1892.



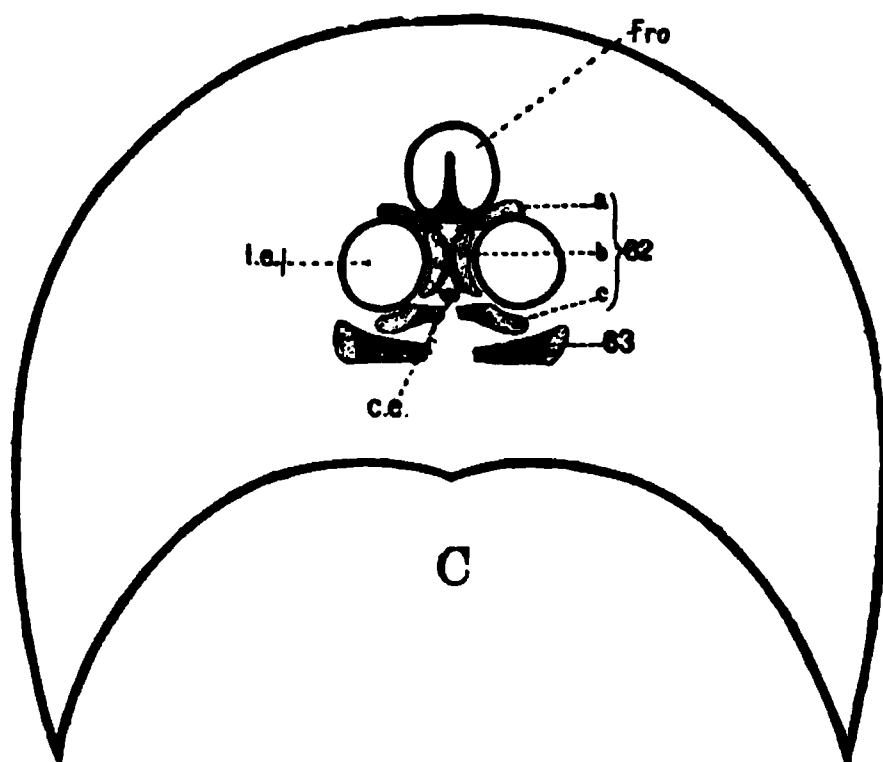
A.

Dorso - ventral muscles on carapace of scorpion (from Miss Beck). 62-65 refer to Miss Beck's catalogue of the scorpion muscles.



B.

Similar muscles on carapace of Eurypterus.



C.

Similar muscles on head shield of a Cephalaspid. l.e, lateral eyes; c.e, central eyes; Fro, narial opening.

FIG. 8.

forms which are looked upon as fish because of the bone tissue in their upper and lower head shields, forms which in every respect are exactly of the kind which ought to have existed according to my theory, as is explained fully in Part VIII., dealing with the palæontological evidence. Here it is sufficient to give a picture of the dorsal head shield of *Thyestes verrucosus* (fig. 9) and of *Tremataspis Mickwitzi* (fig. 10), taken from Rohon's paper, to show how the two lateral eyes were situated close on each side of the mid-dorsal line in these Eurypterid-like fishes, in the very position where they must have been if the eye-muscles were derived from the dorso-ventral somatic muscles of a Eurypterid ancestor.

In Lankester's<sup>1</sup> words, one of the characteristics of the Osteostraci (Cephalaspis, Auchenaspis, etc.), as distinguished from the Heterostraci (Pteraspis), are the large orbits placed near the

## L

FIG. 9. —Dorsal head shield of *Thyestes* (*Auchenaspis*) *verrucosus* (from Rohon).  
 Fro, narial opening; le, lateral eyes; gl, glabellum or plate over brain;  
 Occ, occipital region.

centre of the shield. The apparent exception of *Thyestes* mentioned by him is no exception, for orbits of the same character have since been discovered, as is seen in fig. 9. In fig. 8c I give an outline of the frontal part of the head shield of a Cephalaspid, in which I have drawn the eye-muscles as in the other two figures.

<sup>1</sup> A Monograph of the Fishes of the Old Red Sandstone of Britain, by J. Powrie and E. Ray Lankester. Part 1, The Cephalaspidae, Palæontographical Society, 1868, p. 6.

Next comes the question of the superior oblique muscle and the trochlearis nerve. Why does this nerve alone of all the nerves in the body take the peculiar position it always does take? The only suggestion that I know of which sounds reasonable and worth consideration is that put forward by Fürbringer,<sup>1</sup> which is an elaboration of the original suggestion of Hoffmann.

Hoffmann<sup>2</sup> suggested in 1889 that the trochlearis nerve represented originally a nerve for a protecting organ of the

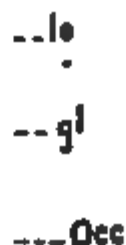


Fig. 10.—Dorsal head shield of *Tremataspis Mickwitzi* (from Rohon). Fro, narial opening; le, lateral eyes; gl, glabellum plate over brain; Occ, occipital spine.

pineal eye, which became secondarily a motor nerve for the lateral eye as the pineal eye degenerated.

Fürbringer (p. 681) differs from Hoffmann in that he considers that the nerve was originally a motor nerve, and was not transformed from sensory to motor, yet thinks Hoffmann's suggestion in the right direction.<sup>3</sup>

<sup>1</sup> "Ueber d. Spino-occipitalen Nerven d. Selachier und Holocephalen," *Festsch. f. Carl Gegenbaur*, p. 681, 1897.

<sup>2</sup> *Zool. Anzeig.*, xii. p. 337-339.

<sup>3</sup> He says:—Ich bin geneigt, den *M. obliquus superior* von einem alten Muskel abzuleiten, der ursprünglich mit dem ihm benachbarten Muskel der Gegenseite für die Bewegung des Parietalauges (dessen langer Nerv die frühere Beweglichkeit noch jetzt andeutet) bestimmt war und mit der sekundären Rückbildung desselben und der höheren Ausbildung der paarigen Augen neue aberrative Muskelemente (beigleichzeitigen successiven Schwund der alten dem parietalen Augen zugehörigen) hervorgehen liess, welche unter Kreuzung und dorsaler antimerer Ueberwanderung sich ganz in den Dienst der bleibenden Augen der Gegenseite stellten, somit eine Muskelwanderung zu statuiren, welche noch jetzt aus der als peripher zu beurtheilenden Kreuzung der beiden Nn. trochleares abgelesen werden kann, auch für die auffallend späte ontogenetische Ausbildung des *M. obliquus superior* und N. trochlearis, dessen primitives Verhalten (Deiters, Golgi) und die grossen Schwier-



Fürbringer points out that the crossing of the trochlearis is not a crossing of fibres between two centres in the central nervous system, but may be explained by the shifting of the peripheral organ, *i.e.* the muscle, from one side to the other, and that the nerve has followed this shift; consequently, says Fürbringer, the course of the nerve indicates the original position of the muscle, and therefore he imagines that the ancestor of the superior oblique muscle was a muscle the fibres of which were attached in the mid-dorsal line, and interlaced with those of the other side, the two muscles thus forming an arch through which the nervous system with its central canal passed; then, for the sake of getting a more efficient pull, the crossing muscle fibres became more definitely attached to the opposite side of the middle line, and finally obtained new attachment on the opposite side, with the obliteration of the muscular arch; the nerve on each side, following the shifts of the muscle, naturally took up the position of the original muscular arch, and so formed the trochlear nerve, with its dorsal crossing. This explanation of Fürbringer's was associated by him with movements of the median pineal eyes, the length of their nerve even yet indicating their previous mobility. This assumption is not to my mind necessary. The length of the nerve is certainly no indication of mobility, for in *Limulus* and the scorpion group the nerve to each median eye is remarkably long, yet they are immovably fixed in the carapace. All that is required is a pair of dorso-ventral muscles belonging to the segment immediately following the group of segments represented by the oculomotor nerves, the fibres of which should cross the mid-dorsal line at their attachment; for, seeing that the lateral eyes were originally so near this position, it follows that such muscles might form part of the muscular group belonging to the lateral eye without having previously moved the pineal eyes. In fact, Fürbringer's explanation requires as starting-point that the pair of muscles which ultimately become the sup.-oblique should have the exact

igkeiten, mit denen gerade hier die embryologische Untersuchung zu kämpfen hat, eine gewisse Illustration abgiebt. Selbstverständlich will dieser Versuch der Erklärung nur eine Idee, ein Programm für künftige Untersuchungen sein; doch glaube ich, dass diese mit der Thatsache der peripherischen Ueberkreuzung der beiden Nn. trochleares und der Ausbildung der M. obliqui superiores aus dem somitischen Material der Gegenseite zu rechnen haben werden."

position of the pair of dorso-ventral muscles in the scorpion called by Miss Beck the anterior dorso-plastron muscles (63) which I have named the oblique muscles. Here, and here only, do we find an interlacement across the mid-dorsal line of the fibres of attachment of the muscles on the two sides, in consequence of which this pair of muscles is described by her as forming an arch encircling the alimentary canal and dorsal vessel; if then, as I have previously argued, the primitive plastron formed a pair of trabeculæ, and the nervous system grew round the alimentary canal, such an arch would encircle the tubular central nervous system of the vertebrate.

Still more striking is this pair of muscles in *Phrynos* (63) in fig. 5, where we see how the arch formed by them almost touches the posterior extremity of the supra-oesophageal brain mass, crossing therefore over the beginning of the stomach region of the animal; the angle formed by the arch is much more obtuse than that formed in the scorpion, so that an actual crossing of the muscle fibres has taken place at the place of attachment to the carapace. Also, only the part nearest the carapace is muscular, the rest forming a long tendinous prolongation of the plastron wall (the primordial cranium), as seen in fig. 5.

This muscle pair is, as it should be, the pair of dorso-ventral muscles belonging to the segment immediately following on the group of segments represented by the recti muscles, *i.e.*, according to previous argument, the segment belonging to the sixth pair of locomotor appendages or ectognaths; a muscle, therefore, which would arise in the vertebrate from the mandibular, and not from the premandibular cavity. A similar muscle probably existed in *Eurypterus*, and, as in the case of the formation of the oculomotor group, derived from the recti group of the scorpion, would form the commencement of the superior oblique muscle in *Thyestes* and *Tremataspis*.

It is instructive to notice that the original position of attachment of this muscle is naturally posterior to that of the ocular group of muscles, and that Fürbringer,<sup>1</sup> in his description of the eye-muscles of *Petromyzon*, asserts that this muscle in this primitive vertebrate form is not attached as in other vertebrates, but is posterior to the other muscles, so that he calls it the

<sup>1</sup> *Op. cit.*, p. 705.

posterior rather than the superior oblique. The nature of the change by which the muscle known in the scorpion as the anterior dorso-plastron muscle (63) was probably converted into the superior oblique muscle of the vertebrate, is represented in the drawings fig. 11, in which also are indicated the dwindling of the median eyes, and the progressive superiority of the lateral eyes, as well as the transformation of the recti muscle group of the scorpion into the muscles supplied by the oculomotor nerve of the vertebrate.

With respect to the external rectus muscle, it follows naturally that if the muscles (64) and (65) are to follow suit with

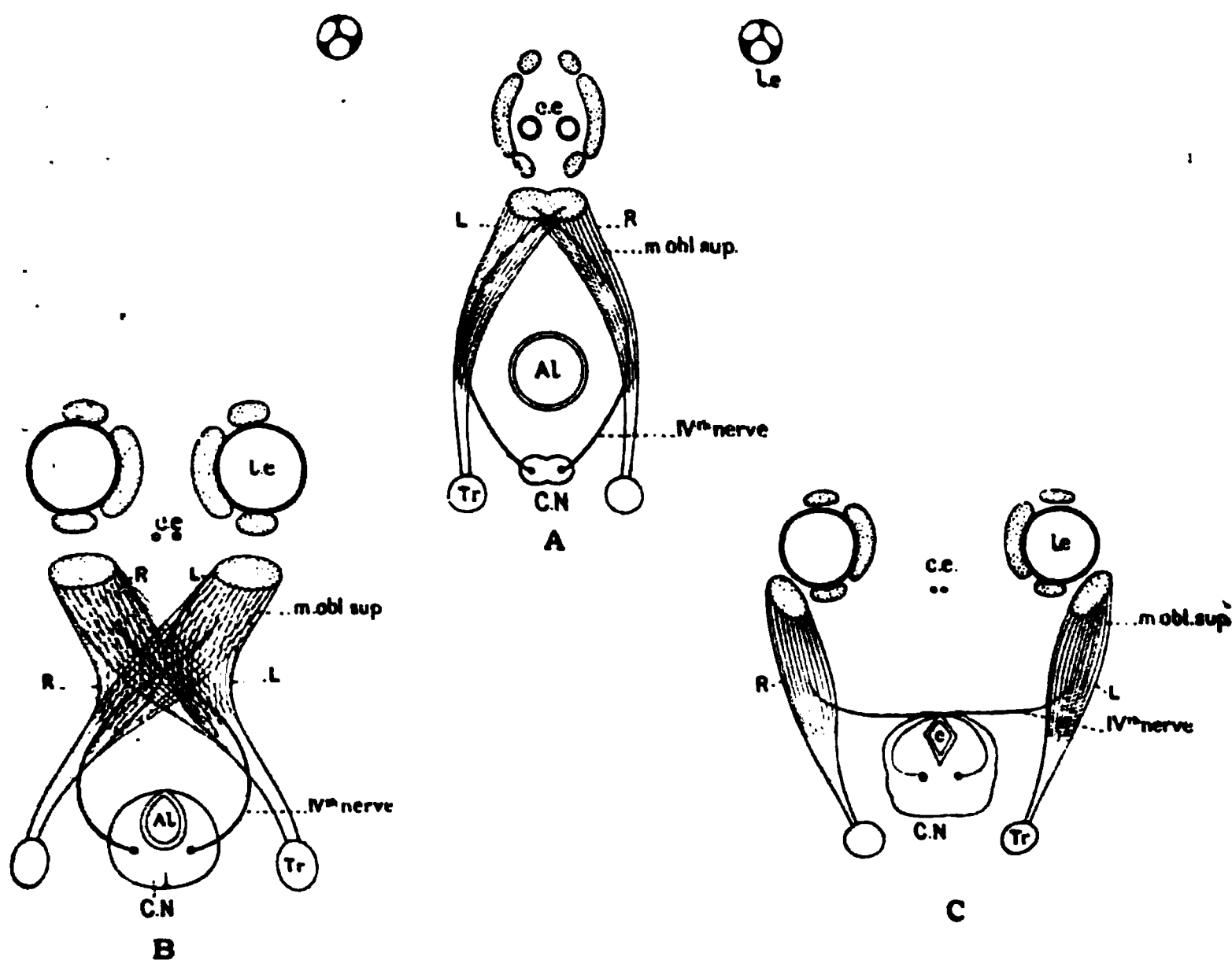


FIG. 11.—A, Diagram of position of oblique muscle in scorpion.

B, Diagram of transition stage.

C, Diagram of superior oblique muscle in vertebrate. le, lateral eyes; ce, central eyes; CN, central nervous system; AL, alimentary canal; c, aqueductus Sylvii.

the rest of the group, and become attached to the lateral eyes, they must take up an external position; these two muscles, which always run together as seen in fig. 8A, the one belonging to the prosoma, and the other to the mesosoma, are represented

by the mandibular muscle of Miss Platt and the external rectus, the former derived from the walls of the last pro-otic head cavity, the latter from the foremost of the opisthotic head cavities.

Such, then, is the simple explanation of the origin of the eye-muscles which follows from my theory, and we see that the successive alterations of the position of the orbit, and therefore of the globe of the eye with its muscles, as we pass from Thyestes to man, is the natural consequence of the growth of the frontal bone, *i.e.*, of the brain.

### *Summary of Part V.*

I would, then, interpret the combined evidence of the anatomy, development, and physiology of the trigeminal nerve group as follows:—

The trigeminal nerves, as far as their splanchnic part is concerned, originally supplied seven separate appendages, of which the first pair were of the nature of antennæ, and the last pair formed the lower lip or metastoma; the remaining five appendages were originally locomotor, tactile, and masticatory. Of these appendages, the muscles belonging to the foremost have dwindled away, those of the last two only remaining strong, and developing to form the masticatory group of muscles innervated from the well-marked motor centre, the *nucleus masticatorius*. The oculomotor nerves originally supplied the dorso-ventral segmental somatic muscles belonging to the 2nd, 3rd, 4th, 5th prosomatic segments, *i.e.*, to the endognathal segments, while the trochlear nerves supplied the corresponding somatic muscles of the segment belonging to the sixth pair of locomotor appendages, *i.e.*, the ectognathal segment. The abducens nerves belonged originally to the mesosoma, and supplied the foremost dorso-ventral mesosomatic muscles; these muscles, however, took up a prosomatic position, and were retained for the service of the lateral eyes.

The actual evidence afforded by *Ammocoetes* of the presence of these appendages will be considered in Part VII. after I have given the evidence as to the nature of the old mouth and olfactory organ.

Such, then, appears to me to be the interpretation of the embryological evidence of segments in the vertebrate head, as deduced from the mesoderm segmentation; and I cannot see how it is possible for ontogeny to give us a clearer instance of the past history of organs than is done in this case. She marks out in the vertebrate each mesosomatic branchial segment, with its well-defined coelomic cavity, just as though it were a *Limulus* we were watching; she differentiates between the mesosomatic branchial and prosomatic non-branchial segments; and where, as in the premandibular region, the appendages have become small and obscure, there the indications of separate segments are also obscure; where, as in the mandibular region, they have kept large, or even grown and developed in the vertebrate group, there the segmental muscles are well developed, both in the ventral group as well as in the dorsal.

It is because of the dwindling of the ventral appendages in the foremost region that Neal can say that the mesomeres in the head afford the most trustworthy criterion of metamerism. The dorsal segments (neuromeres and mesomeres) must be regarded as more conservative than the ventral (branchiomic or splanchnic) segmentation; the lost elements are chiefly the ventral ones.<sup>1</sup>

It is because of the loss of the segmental somatic muscles in the hindmost region, and the permanence of the appendages here, that Gegenbaur concludes that the visceral arches are the essential criteria of cephalic metameres.

For this reason, there is the apparent discrepancy between Branchiomerie and Mesomerie, a discrepancy which did not originally exist, the reason for which can be summed up in the short sentence—this discrepancy is due, on the one hand, to the dwindling and ultimate disappearance of the foremost locomotor appendages, and on the other, to the disappearance of the ventro-dorsal somatic segmental muscles, except those which have been preserved in order to move the eyes.

<sup>1</sup> Neal, *op. cit.*, p. 270.

PART VI.—THE OLD MOUTH AND THE OLFACTORY ORGAN:  
THE MEANING OF THE FIRST NERVE.

I will commence this part, as in Part V., by considering the nature of the problem presented by the Merostomata; that is to say, the nature of the mouth and the parts surrounding it in the group from which I suppose an Ammocetes-like form to have sprung. I will therefore consider, in the first place, the nature of the mouth in the living scorpions and their allies. The best paper by far with which I am acquainted on this subject is a paper by Croneberg,<sup>1</sup> published in 1880, in which he considers the views of previous observers, and shows how his conclusions are borne out by the study of the mouth parts in the Scorpions, in the Solpugidæ, in the Mygalidæ, in the Phalangidæ, in the Chelifers.

*The Nature of the Camerostome.*

The main question in dispute is the nature of the so-called upper lip or camerostome, called also in many cases the rostrum. This organ, according to Croneberg, is in reality a paired appendage, preoral in position, which represents the first pair of antennæ in the Crustacea; it is conspicuously a paired antennæ-like organ in Galeodes, and he considers that the paired apodemes which pass from it into the interior of the thorax, called by Lankester the median preoral entosclerite, correspond to the apodemes, *i.e.*, entosclerites of the rest of the thoracic appendages; he also shows that embryologically this rostrum or camerostome arises as a pair of appendages similar to the other appendages. This last observation of Croneberg has been confirmed by Brauer<sup>2</sup> in 1894, who describes the origin of the upper lip, as he calls it, in very similar terms, without, however, referring to Croneberg's paper. Croneberg further shows that this foremost pair of antennæ not only forms the so-called upper lip or camerostome, but also a lower lip, for from the basal part

<sup>1</sup> "Ueber die Mundtheile der Arachniden," by A. Croneberg, *Archiv. f. Naturgeschichte*, Jahrgang 46, 1880, p. 285.

<sup>2</sup> *Op. cit.*, p. 360.

of the camerostome there projects on each side of the pharynx a dependant accessory portion, which in some cases fuses in the middle line and forms, as it were, a lower lip. The entosclerite belonging to this dependant portion is apparently the postoral entosclerite of Lankester and Miss Beck.

At the base of the tubular passage so formed by this modified first pair of antennæ is found the true mouth, opening directly into the dilated pharynx, the muscles of which enable the act of

cam

pr.en

FIG. 12.—Dorsal view of brain and camerostome of *Galeodes*. *cam.*, camerostome; *pr. ent.*, preoral entosclerite; *l.l.*, dependant portion of camerostome; *ph.*, pharynx; *al.*, alimentary canal; *n.op.*, median optic nerves; *pl.*, plastron; *v.c.*, ventral nerve chain; 2, 3, second and third appendages.

suction to be carried out; from the pharynx there passes the narrow œsophagus, completely closed in by the supra- and infra-œsophageal nerve masses.

Huxley<sup>1</sup> also describes the mouth of the scorpion in precisely the same position.

In order to convey to my readers the antennæ-like character of the camerostome in *Galeodes*, and its position, I give a figure

<sup>1</sup> *Op. cit.*

(fig. 12) of the organ from its dorsal aspect, after removal of the chelicerae and their muscles. The figure shows also its position with respect to the supra-oesophageal ganglion (*gl. supr.-œs.*) and the infra-oesophageal ganglionic mass (*gl. infr.-œs.*) A side view of the same organ is given in fig. 13 to show the feathered termination of the camerostome, and the position of the dependent accessory portion (*l.l.*) (Croneberg's untere Anhang)

of ant

FIG. 13.—Lateral view of brain and camerostome of Galeodes. *gl. supr.-œs.*, supra-oesophageal ganglion; *gl. infr.-œs.*, infra-oesophageal ganglion. The rest of the lettering same as in fig. 12.

with its single long antenna-like feather. In both figures the alimentary canal (*al.*) is seen issuing forth from the conjoined supra- and infra-oesophageal mass.

As is seen in the figure, the bilateral character of the rostrum, as Croneberg calls it, is apparent not only in its feathered extremity but also in its chitinous covering, the softer median dorsal part being bounded by two lateral plates of hard chitin, which meet in the middle line near the extremity of the organ. In all the members of the scorpion group, as is clearly shown in Croneberg's figures, the rostrum or camerostome is built up on the same plan as in Galeodes, though the antennæ-like character may not be so evident.

When we consider that the first pair of antennæ in the Crustaceans are olfactory in function, Croneberg's observations amount to this :—

In the Arachnids and their allies the first pair of antennæ form a preoral passage or tube, olfactory in function; the small



mouth, which opens directly into the pharynx, being situated at the end of this olfactory passage.

Croneberg's observations and conclusions are distinctly of very great importance in bringing the Arachnids into line with the Crustaceans, and it is therefore most surprising that they are absolutely ignored by Lankester and Miss Beck in their paper published in 1883, in which Latreille only is mentioned with respect to this organ, and his term camerostome, or upper lip, is used throughout, in accordance with the terminology in Lankester's previous paper.<sup>1</sup> That this organ is not only a moveable lip or tongue, but essentially a sense organ, almost certainly of smell and taste, as follows from Croneberg's conclusions, is shown by the series of sections which I have made through a number of young *Thelyphonus* which were found on their mother's back in a termite's nest by Mr Haviland, whom I here take the opportunity of thanking for his kindness in presenting me with the mother and young ones.

I give in fig. 14 a sagittal median section through the head end of the animal, which shows clearly the nature of Croneberg's conception. At the front end of the body is seen the median eye (*ce.*), *o* is the mouth, *ph.* the pharynx, *æs.* the narrow œsophagus, compressed between the supra-œsophageal (*supr.-æs.*) and infra-œsophageal (*infr.-æs.*) brain mass, which opens into the large alimentary canal (*Al.*); *olf. pass.* is the olfactory passage to the mouth, lined with thick-set, very fine hairs, which spring from the hypostome (*hyp.*), as well as from the large conspicuous (*cam.*) camerostome, which limits this tube anteriorly. The space between the camerostome and the median eye is filled up by the massive chelicerae, which are not shown in this section, as they begin to appear in the sections on each side of the median one. The muscles of the pharynx and the muscles of the camerostome are attached to the preoral entosclerite (*pr. ent.*). The postoral entosclerite is shown in section as *post. ent.* The dorsal blood-vessel or heart is indicated at *H.*

In fig. 15 I give a transverse section through another of the same litter, to show the nature of this olfactory tube when cut across. Both sections show most clearly that we are dealing here with an elaborate sense organ the surface of which is

<sup>1</sup> "Limulus an Arachnid," *Q. J. of Micro. Sci.*, vol. xxi., 1881, p. 529. 3

partly covered with very fine long hairs, partly, as is seen in the figure, is composed of long, separate, closely-set sense rods (*bat.*), well protected by the long hairs which project on every side in front of them, which recall to mind Bellonci's figure<sup>1</sup> of the *batonets olfactives* on the antennæ of *Sphæroma*. Finally, we have the observation of Blanchard quoted by Huxley,<sup>2</sup> to the effect that this camerostome is innervated by nerves from

*pr en:*                      *roa*

FIG. 14.—Median sagittal section through a young *Thelyphonus*.

the supra-oesophageal ganglia which are clearly bilateral, seeing that they arise from the ganglion on each side and then unite to pass into the camerostome; in other words, paired olfactory nerves from the supra-oesophageal ganglia.

This olfactory tubular passage so formed is bounded laterally and posteriorly by the sterno-coxal processes of the 2nd or more prosomatic appendages, and by the pro-sternite when present; anteriorly by the two chelicerae with their strong gripping forceps; so that, if we look into the so-called mouth of the scorpion, we see the camerostome projecting from the roof of the tube and nearly dividing the tube into two parts. These sterno-coxal processes were in *Limulus* and the Eurypterids markedly masticatory in function, forming the foot-jaws. In *Buthus* and the scorpions the sterno-coxal processes of the 2nd,

<sup>1</sup> "System nerveux et organes des sens du *Sphæroma serratum*," *Arch. Ital. de Biol.*, vol. i. p. 176.

<sup>2</sup> *Op. cit.*, p. 251.

3rd, and 4th prosomatic appendages take part in surrounding the olfactory tubular passage; in *Thelyphonus* only the processes of the 2nd pair of prosomatic appendages, the pro-sternite

FIG. 15.—Transverse section through the olfactory passage of a young *Thelyphonus*. 1 and 2, sections of first and second appendages.

not being present. In *Limulus* a conjoined pro-mesosternite (fig. 1, *end*) forms the median ventral wall, to which the sterno-

--cart

FIG. 16.—Transverse section through the olfactory passage of *Ammocetes*.  
*cart.*, nasal cartilage.

coxal processes are attached, and in *Phrynus* (fig. 24) and *Mygale* a well-marked pro-sternite and meso-sternite are

present, forming the posterior limit of the olfactory opening. In the former these sternites, curiously enough, carry short antenna-like projections, as in fig. 24A.

That the mouth parts of *Eurypterus* were partly like those of the scorpion and partly like those of *Limulus*, appears to me certain from the observations of Holm; the difference of these sea scorpions from the living scorpions being due essentially to the development of the metastoma. All observers are agreed that this lip plate was freely movable. Nieskowski<sup>1</sup> considered that the movement of the metastoma was entirely in a vertical direction, whereby the cleft which is seen between the basal joints of all the pairs of locomotor appendages could be closed from behind. Woodward<sup>2</sup> says it no doubt represents the *labium* and served more effectually to enclose the posterior part of the buccal orifice, being found exterior to the toothed edges of the ectognaths or maxillipedes. Schmidt agrees with Nieskowski, and looks on the metastoma as forming a lower lip within which the bases of the ectognaths worked.

Quite recently Gerhard Holm<sup>3</sup> has worked over again the very numerous specimens of *Eurypterus Fischeri* which are obtainable at Rootziküll, and has thrown new light on the relation of the metastoma to the mouth parts. His preparations show clearly that the true lower lip of *Eurypterus* was not the metastoma, for when the metastoma is removed another plate situated internally to it is disclosed, which, in his view, corresponds to the sternite between the bases of the pro-somatic appendages in *Limulus*, i.e., to the sternite called by Lankester the pro-mesosternite. This inner plate formed with the metastoma and the ectognaths a chamber closed posteriorly within which the bases of the ectognaths worked. In other words, the removal of the metastoma discloses in *Eurypterus* the true anterior ventral surface of the animal resembling that of *Limulus* or of the scorpion group, with its pro-mesosternite and laterally attached gnathites or sterno-coxal processes. To

<sup>1</sup> "Der *Eurypterus Remipes* aus den obersilurischen Schichten der Insel Oesel," *Arch. f. d. Naturkunde Liv-, Ehst- und Kurlands*, Bd. 3, 1<sup>ste</sup> ser., 1858, p. 317.

<sup>2</sup> "British Fossil Merostomata," *Palæontological Society*, 1866-1878, p. 39.

<sup>3</sup> *Op. cit.*

this inner plate or pro-mesosternite Holm gives the name of *endostoma*.

To the anterior edge of the endostoma a thinner membrane is attached which passes inwards in the direction of the throat, and forms, therefore, the lower lip of the passage of the mouth. This membrane bears upon its surface a tuft of hairs, which he thought were probably olfactory in function. Consequently, in his preliminary communication,<sup>1</sup> he describes this lower lip as forming in all probability an olfactory organ; in his full communication he repudiates this suggestion, because he thinks it unlikely that such an organ would be situated within the mouth. I feel sure that if Holm had read Croneberg's paper and seen how the true mouth in all the scorpion group is situated at the base of an olfactory passage, he would have recognised that his first suggestion is in striking accordance with the nature of the entrance to the mouth in other scorpions.

That Eurypterus also possessed a camerostome seems to follow of necessity from its evident affinities both with Limulus and the scorpions.

We see, in fact, that the mouth of these old sea scorpions was formed after the fashion of Limulus, surrounded by masticatory organs in the shape of foot-jaws, and yet foreshadowed that of the scorpion.

If only the present-day scorpions possessed a metastoma, we should be able to compare their mouth parts very closely with those of Eurypterus. Unfortunately, there does not seem to be much chance of finding a metastoma among living scorpions. As far as I know, the only evidence of anything at all approaching to a metastoma is given by Bruce<sup>2</sup> in a short account of a Phrynus from the Bahama Islands, brought by Dr Orr. He says:—"The ventral surface of the thorax of the adult closely resembles that of Limulus, especially in the existence of a curved process on the inner side of the coxal joint of the last thoracic appendage, corresponding to a similar process on the coxal joint of the last appendage of Limulus. Traces of similar processes occur on the 4th and 5th thoracic appendages.

<sup>1</sup> "Ueber eine neue Bearbeitung des *Eurypterus Fischeri*," *Bull. d. l'Acad. Imp. d. Sci. d. St Petersburg*, 1896, t. iv. p. 369.

<sup>2</sup> A. J. Bruce, *Johns Hopkins University Circular*, Dec. 1886, p. 47.

Also a paired structure occurs posterior to the last pair of thoracic appendages, corresponding to the chilaria or metastoma of *Limulus*."

I have been unable to find any further information about this particular species of *Phrynus* or to obtain any specimens. I should be very grateful to any one who could give me information on the subject, or obtain for me specimens similar to those thus briefly described by Bruce.

The best method of obtaining a clear conception of the arrangement of the mouth parts in the Eurypterids is by means of an ideal sagittal section through the animal. In order to obtain this, I propose to combine the information obtained by Holm with actual sagittal sections through *Limulus* and the scorpion group. In fig. 17A I give a sagittal section through *Limulus* to show the arrangement of parts and the small pair of chilaria which by its fusion and forward growth form the metastoma. In this figure I have indicated the position of the prosomatic appendages and their nerve supply, also the coxal gland, which sends prolongations into the coxæ of the 2nd, 3rd, 4th, and 5th appendages.

By the combination of this figure with that of *Thelyphonus* (fig. 14), already mentioned, we obtain fig. 17B, which represents an ideal section through a Eurypterid, in which I have drawn an olfactory passage and represented a commencing suctorial mouth with a pharynx after the scorpion fashion, and have indicated the position of the endognaths, ectognath, and chilaria in the same manner as in fig. 17A. In this case I have concentrated the coxal gland near the pharynx, because the endognaths, with which alone, judging from *Limulus*, the coxal gland has connection, are bunched close together around the olfactory orifice, and have, therefore, a concentrated anterior position. For the same reason I have drawn the appendage nerves of the endognaths close together, forming practically one nerve bundle, while the nerve to the large ectognath and metastoma remain separate as in *Limulus*.

The different parts represented in this section are :—

*Cam.* = rostrum or camerostome = fused olfactory antennæ.

*Hyp.* = lower lip of olfactory tube or hypostoma<sup>1</sup> = lower pen-

<sup>1</sup> In Part II. of this series of papers (this *Journ.*, vol. xxxii. p. 561) I have used the term hypostoma to indicate what is here called the endostoma.

dent part of the fused olfactory antennæ (Croneberg's *untere Anhang*).

*End.* = inner lip of the metastomal or accessory oral (*or.*) chamber or endostoma = the pro-mesosternite of *Limulus*, together with the sterno-coxal processes of the endognaths (2, 3, 4, 5).

7 = outer lip of the metastomal accessory oral (*or.*) chamber or metastoma = the last pair of prosomatic appendages, to which the basal joint of each ectognath (6) was attached.

*Olf. pass.* = olfactory pit or tubular olfactory passage to the mouth (*o.*), which opens into the pharyngeal chamber (*ph.*), from which arises the narrow œsophagus (*œs.*) leading into the large alimentary canal (*Al.*).

*Cox. gl.* = coxal gland.

*C. e.* = the median eyes.

*Op.* = the optic part of the supra-œsophageal ganglion.

*Ol.* = the olfactory part of the supra-œsophageal ganglion.

*Gl. infr.-œs.* = the infra-œsophageal ganglion, upon which are indicated the prosomatic ganglia giving origin to the nerves of the prosomatic appendages (2, 3, 4, 5, 6, 7), and the first mesosomatic ganglion, giving origin to the opercular nerves. I have not attempted to put in the nerves to the first pair of appendages (1) or chelicerae.

8 = genital part of the operculum.

8' = branchial part of the operculum.

9 = second branchial segment.

10 = third branchial segment.

I have also, on the ground of the similarity of the appearance of *Eurypterus* with living scorpions, inserted the position of the *m. obliquus* (*m. obl.*).

Suppose now, according to my theory, that the mouth (*o*) becomes closed, nothing more; then immediately in all its essential parts the figure represents a sagittal section through the early condition of *Ammocoetes*, as pictured by Dohrn and Kupffer. In fig. 17, C, I give such a picture, in which I have inserted the nerve masses of the more advanced stage and indicated the origin of the cranial nerves from centres resembling those of higher vertebrates.



**C**

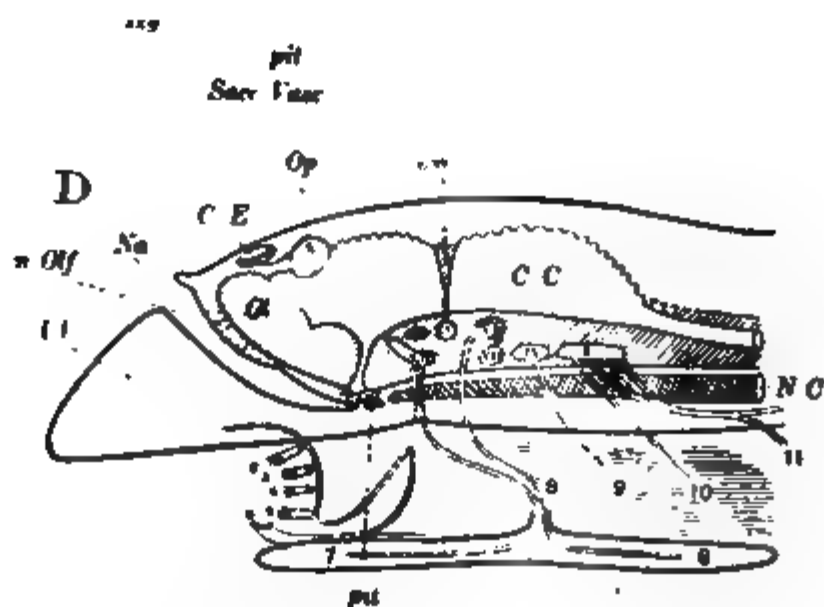


FIG. 17.—Diagram of sagittal median section through  
 A. *Limulus*. B. *Eurypterus*.  
 C. Larval *Ammocetes*. D. Full-grown *Ammocetes*.



The comparison of the two sections shows with remarkable clearness the homologous parts in the two animals:—

1. The olfactory tube (*olf. pass.*) becomes in the young Ammocoetes the tube of the hypophysis (*hy.*), at the bottom of which the palæostoma is supposed by various observers to be situated.

2. The pharynx of the scorpion becomes the saccus vasculosus (*sacc. vasa.*) of the vertebrate; and, owing to its size, gives the reason for the folds of the saccus vasculosus and the so-called glandular appearance.

3. The œsophagus, already compressed between the supra- and infra-œsophageal ganglia, becomes the tube of the infundibulum (*inf.*).

4. The large stomach which is arched over by the pair of muscles (*m. obl.*) becomes the ventricles (*c. c.*), constricted in a similar position by the fourth nerve (IV.).

5. The straight intestine becomes the spinal canal.

6. The median eye, with its nerve from the optic portion of the supra-œsophageal ganglion, becomes the pineal eye (*c. c.*), with its nerve from the so-called ganglion habenulæ.

7. The modified olfactory antennæ, with its nerve from the olfactory part of the supra-œsophageal ganglion, becomes the olfactory plakode (*olf.*), with its nerve from the olfactory part of the brain.

8. The metastomal or accessory oral chamber, formed by the metastoma and the endostoma or promesosternite, becomes the oral or so-called stomodæal chamber of the Ammocoetes, formed by the lower and upper lips.

9. The endostoma or promesosternite, with the sterno-coxal processes or gnathites attached to it, becomes the upper lip with the tentacles attached to it.

10. The metastoma, or 7th pair of prosomatic appendages, to which the ectognaths are attached, becomes the lower lip to which the two large median ventral tentacles, the so-called tongue of Rathke, are attached.

11. The genital operculum, with its median genital process attached in its basal part to the basal part of the metastoma, becomes the thyroid segment, the basal part of which, together with the basal part of the lower lip, forms the septum of the stomodæum.

12. The branchial operculum forms the branchial hyoid segment.

13. The remaining branchial mesosomatic segments form the remaining branchial segments of the *Ammocoetes*.

14. The coxal gland becomes the pituitary body.

15. The nerves to the endognaths, to the ectognaths, and to the metastoma become respectively the tentacular nerves, the tongue nerve, and the lower lip nerve (see Part VII.), just as the nerves to the genital and branchial parts of the operculum become respectively the thyroid and hyoid nerves.

In order to make the lesson of this series of sagittal sections complete, I will finish the series with a drawing of a median sagittal section through the anterior region of a full-grown *Ammocoetes* (fig. 17, D).

The difference between this section and fig. 17, C, is due to the growth of the upper lip, by which the nasal orifice and tube are pushed dorsally, as described by Balfour, and illustrated by Kupffer.

### *The Olfactory Organ of Ammocoetes.*

The olfactory organ of *Ammocoetes* is in the shape of a tube lined with olfactory epithelium enclosed in an outer casing. The shape and arrangement of the epithelium lining this tube is very significant, as throughout it consists of a thicker part and a thinner part, as seen in fig. 16, which represents a transverse section through this tube. The thicker part forms the true olfactory plakode of Kupffer, and the thinner part is formed by the prolongation of the lower lip of the tube of the hypophysis, as described by Kupffer. A horizontal section through the organ shows clearly the same separation into two parts (*cf.* fig. 4, Pl. LVI.). The comparison of such sections with those of the olfactory tube of *Thelyphonus* (fig. 15) leads directly to the conclusion that the thicker projecting part, the olfactory plakode, is the camerostome or conjoined olfactory antennæ of the scorpion group, and the thinner part is the lower lip of the olfactory tube (Croneberg's *untere Anhang*).

Further, just as the termination of the olfactory tube in *Galeodes* and others of the scorpion group demonstrates its

original paired antennæ-like character even in the adult, so also the termination of the nasal tube in *Ammocoetes* demonstrates also its original paired character.

In fig. 3, Pl. LVI., I give a drawing of the dorsal surface of the anterior end of the head of a large *Ammocoetes*, which shows how within the median nasal cup the olfactory organ terminates as two leaflets, between which an open slit leads into the nasal passage. Horizontal sections, such as figs. 18, A and B, and fig. 4, Pl. LVI., demonstrate how by the coming together of the edges of these two leaflets the thinner part of the epithelium lining the nasal tube is formed.

Fig. 4, Pl. LVI., also shows how this nasal tube (*na*) is imbedded in muco-cartilaginous tissue (*m. cart.*), and is partially surrounded by cartilage (*na. cart.*); how also the peculiar connective tissue of the cranial wall (*cr*) abuts against this cartilage posteriorly. This cartilaginous framework is confined to the more dorsal part of the tube, always following the contour of the thickened olfactory epithelium; in other words, it belongs to the camerostome proper, and not to the lower dependent lip. It is also soft cartilage formed, therefore, in connection with muco-cartilage, and not with the tissue of the cranial walls.

It is clear that the olfactory organ of *Ammocoetes* may be regarded as a separate organ, lying close against the median anterior wall of the cranium, the external surface of which has either become merged into the mass of muco-cartilage which exists here, or become cartilaginous. If we were to isolate this organ, and represent the cartilaginous part of the framework by a hard covering, and the muco-cartilaginous part by a softer portion, we should obtain an appearance as in fig. 19, which represents a lateral view of the brain and the nasal organ. Such a figure compares most closely with the camerostome and brain (fig. 13) of *Galeodes* or of the scorpion group if we imagine such brain to have grown larger; and if we take into account the similarity of the internal structure and the fact that the olfactory tube terminates at the infundibulum, we must come to the conclusion that the median olfactory organ of the *Ammocoetes* is simply the camerostome of a scorpion-like animal which has become imbedded in muco-cartilage, bent dorsalwards, and closely pressed against the anterior wall of

the cranium, owing to the forward growth and expansion of the pro-mesosternite to form the upper lip.

The single median position of the olfactory organ in the Cyclostomata, in contradistinction to its paired character in the rest of the vertebrates, has always been a stumbling-block in the

B

FIG. 18, A and B.—Horizontal sections through the olfactory tube of *Ammocetes*, near its external opening.

way of those who desired to consider the Cyclostomata as degenerated Selachians, for the origin of the olfactory protuberance as a single median plakode seemed to indicate that the nose arose as a single organ, and not as a paired organ. On the other hand, the two olfactory nerves of *Ammocetes* compare

absolutely with the olfactory nerves of other vertebrates, and force one to the conclusion that this median organ of *Ammocoetes* arose from a pair of bilateral organs which have fused in the middle line.

The comparison with the camerostome gives a satisfactory reason for its appearance in the lowest vertebrates as an unpaired median organ, and equally so the history of the camerostome itself gives the reason why the olfactory nerves are double,

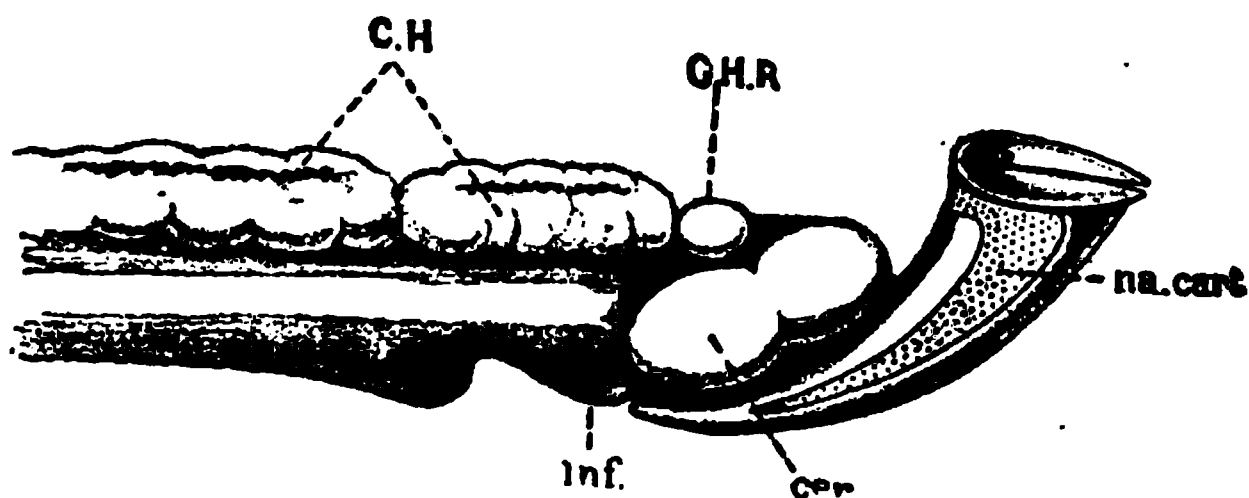


FIG. 19.—Brain and olfactory organ of *Ammocoetes*. *na. cart.*, nasal cartilage; *cer.*, cerebrum; *G.H.R.*, right ganglion habenulæ; *C.H.*, folds of choroid plexus; *inf.*, infundibulum.

why the organ is in reality a paired organ, and not a single median one; so that in a sense the grouping of the fishes into *Monorhinæ* and *Amphirhinæ* has not much meaning, seeing that the olfactory organ is in all cases double.

Yet, again, another peculiarity receives the simplest of solutions, viz., the relation between taste and smell; *i.e.*, the appreciation of flavour; for in our scorpion-like ancestors taste and smell were one: the same organ situated at the entrance of the mouth, over which all food passed, was necessarily an organ of taste, and, as its history shows, being derived from the ancient olfactory antennæ of the great Arthropod group was also the organ of smell, so that the olfactory region of the supra-oesophageal ganglion was necessarily the centre for the appreciation of taste as well as of smell. How conservative this mechanism is, how exactly the olfactive lobes of the Arthropod resemble those of the Vertebrate, is clearly shown by the researches of Bellonci,<sup>1</sup> who concludes that the structure and

<sup>1</sup> Bellonci, "Sur la structure et les rapports des lobes olfactives dans les Arthropodes supérieurs et les Vertébrés," *Archiv. Ital. de Biol.*, vol. 3, 1883, p. 191.

relations of the olfactive lobes of the more highly organised Arthropoda and of the Vertebrates present the same fundamental plan. He points out how exactly the olfactory glomeruli of the higher crustaceans resemble those of vertebrates, and concludes that such extraordinary resemblance occurring in two types of animal so aloof from one another as a crustacean and an amphibian—a resemblance so perfect as to appear to constitute a true morphological homology—is due to a physiological necessity, that similarity of function in the central nervous system carries with it similarity of structure.

Clearly this remarkable resemblance of the structure of the olfactory lobes in the two groups of animals does constitute a true morphological homology; and I would trace an unbroken sequence in the evolution of the foremost sense organs and the first nerve from the olfactory antennules of the crustacean to the camerostome of the scorpion group; from the camerostome of the scorpions to the olfactory organ of *Ammocoetes*; from the olfactory organ of *Ammocoetes* to the olfactory organ of man.

Finally, this homology gives an explanation of Marshall's original view, that the olfactory organ arose as a special sense organ belonging to the series of branchial sense organs, a view which has been urged by Beard and others for both olfactory and auditory organs. This theory of branchial sense organs in the region in front of the branchial region is explainable, as already mentioned, as sense organs belonging to appendages which were not branchial, but were serially homologous with the branchial appendages. The foremost of these appendages were the olfactory antennæ, with the olfactory epithelium as their organ of special sense. In this sense Marshall was right, Beard is right, Dohrn is right; once substitute the word appendage as the segmental unit instead of branchial pouch, then we see how these observations all fit together, all help to build up the conception of the origin of vertebrates in accordance with the lines laid down in this series of papers.

#### *The Old Mouth, or Palæostoma.*

Morphologically the tubular olfactory passage of the scorpion group is quite independent of the mouth, so that if that mouth

were closed and a new food passage formed, the olfactory tube would remain as an independent tube or pit just as is seen in *Amphioxus* and all Vertebrates. The nearest approach to the original condition is seen in *Ammocoetes*, where the olfactory or nasal tube still leads directly to the old mouth or palæostoma.

This conclusion is not only not at variance with the opinion of morphologists, but gives a straightforward, simple explanation why the palæostoma was situated in the very place where they are most inclined to locate it; thus, if we trace the history of the question, we see that Dohrn's original view of the comparison of the vertebrate and the annelid led him to the conception that the vertebrate mouth was formed by the coalescence of a pair of gill slits, and that the original mouth was situated somewhere on the dorsal surface and opened into the gut by way of the infundibulum and the tube of the hypophysis. This also was Cunningham's view as far as the tube of the hypophysis was concerned. Beard in 1888,<sup>1</sup> holding the view that the vertebrates were derived from annelida which had lost their supra-oesophageal ganglia, and that therefore there was no question of an oesophageal tube piercing the central nervous system of the vertebrate, explained the close connection of the infundibulum with the hypophysis by the comparison of the tube of the hypophysis with the annelidan mouth, so that the infundibular or so-called nervous portion was a special nervous innervation for the original throat, just as Kleinenberg had shown to be the case in many annelida. Beard therefore called this opening of the hypophysial tube the old mouth or palæostoma. Recently, in 1893, Kupffer<sup>2</sup> has also put forward the view that the hypophysial opening is the palæostoma, basing this view largely upon his observations on *Ammocoetes* and *Acipenser*. The tube which Kupffer considers to be the tube of the hypophysis in *Ammocoetes*, lies at first just behind the median olfactory protuberance or plakode, as shown in fig. 17c. Subsequently, by the great enlargement of the upper lip, this tube, as already explained, becomes the nasal tube. According, then, to Kupffer, the nasal tube of the *Ammocoetes* is derived

<sup>1</sup> Beard, "The Old Mouth and the New," *Anat. Anzeig.*, 1888, p. 15.

<sup>2</sup> C. v. Kupffer, *Stud. z. vergleich. Entwickl. geschich. des Kopfes d. Kranioten*, Heft 1. *Die Entwickl. d. Kopfes v. Acipenser*, München, 1893.

directly from the primitive mouth tube. His grounds for this supposition are based not only on the close connection of the termination of this tube with the extremity of the hypoblastic notochord, as pointed out by Dohrn, but upon the contiguity of this tube with the preoral elongation of the alimentary canal; and, indeed, in *Myxine* this nasal tube is not closed but does actually open into the alimentary canal. Such opening into the gut in *Myxine* is not supposed to be a primitive condition, but to have arisen secondarily, and has much the same kind of significance as the opening of the nose into the throat in the higher vertebrates. Kupffer believes that the walls of this tube form the glandular tissue of the hypophysis or the pituitary body, as, indeed, Scott had previously stated to be the fact in *Petromyzon*. Bela Haller, in a recent paper,<sup>1</sup> criticises Kupffer's statements, and considers that the nasal tube and the glandular hypophysis are disconnected throughout, the latter being formed quite separately. Bela Haller's view appears to me the right one; I shall therefore consider the pituitary body separately, and at this point simply emphasise the fact that in this primitive vertebrate a tube is formed at the anterior ventral surface of the body, which terminates in close connection with the extremity of the notochord, with the tongue-like prolongation of the gut, and with the saccus vasculosus. At the termination of this tube, the palæostoma was situated, according to Beard and Kupffer, in precisely the very spot where the palæostoma must have been situated according to my view.

Here, again, then, we see how ontogeny recapitulates phylogeny, how strikingly the remarkable peculiarities of the development of the olfactory organ in this primitive vertebrate all receive a simple phylogenetic explanation on the theory that the *Ammocoetes* has arisen from the *Eurypterid*.

### *Meaning of the Pituitary Body.*

There remains for consideration the glandular portion of the hypophysis or pituitary body. This gland undoubtedly arises posterior to the hypophysial tube or Rathke's pouch, and, as

<sup>1</sup> B. Haller, "Untersuch. üb. d. Hypophyse u. d. Infundibul. organe," *Morph. Jahrbuch*, Bd. xxv. p. 31, 1898.



already mentioned, is supposed by Kupffer to be formed from the posterior wall of this pouch. More recently, as pointed out in Haller's paper, Nusbaum,<sup>1</sup> who has investigated this matter, finds that the glandular hypophysis is not formed from the walls of Rathke's pouch, but from the tissue of the rudimentary connection or stalk between the two premandibular cavities, which becomes closely connected with the posterior wall of the Rathke's pouch, and becoming cut off from the rest of the premandibular cavity on each side, becomes permanently a part of the hypophysis anlage. Nusbaum agrees with Kupffer that these premandibular cavities are formed from entodermal diverticula of the gut, and therefore that the glandular hypophysis is derived from cells of the gut wall.

The importance of Nusbaum's investigation consists in this, that he derives the glandular hypophysis from the connecting stalk between the two premandibular cavities, and therefore forms it from the walls of the ventral continuation of this cavity on each side. From what has already been said, it appears to me clear that Kupffer is wrong in supposing that the premandibular cavity is a visceral pouch, and that therefore the eye muscles are the muscles of visceral arches; the question has been discussed in an able manner by Neal,<sup>2</sup> who entirely agrees in his own observations with those of Goette in flatly contradicting Kupffer's statements as to the development of the premandibular cavities in *Ammocoetes* from diverticula of the alimentary canal; he gives illustrations of the manner of formation of the premandibular cavities and their connecting stalk in embryos of *Squalus acanthias*, and concludes that "there exists not the faintest shadow of evidence that the mass of cells which forms in its lateral part the premandibular cavities, and in its median part their connecting stalk, represents entodermal diverticula." We may therefore consider the following interpretation of Nusbaum's investigations as by far the most probable, if not most certainly true.

The coelomic cavity known as the premandibular cavity divides into a dorsal and a ventral part; the walls of the dorsal part

<sup>1</sup> J. Nusbaum, "Einige neue Thatsachen zur Entwick. geschich. d. Hypophysis Cerebri bei Säugethieren," *Anat. Anzeig.*, Bd. xii., 1896.

<sup>2</sup> *Op. cit.*, pp. 199-205.

give origin to the somatic muscles belonging to the oculomotor nerve, while the walls of the ventral part on each side form the connecting stalk between the two cavities, and give origin to the glandular hypophysis.

Now, as already pointed out, the premandibular cavity is homologous with the 2nd prosomatic coelomic cavity of *Limulus*, and this 2nd prosomatic coelomic cavity divides according to Kishinouye<sup>1</sup> into a dorsal and a ventral part; and further, the walls of this ventral part form the coxal gland. Both in the vertebrate, then, and in the *Limulus* we find a marked glandular tissue in the corresponding position, and the conclusion is forced upon us that the glandular hypophysis was originally the coxal gland of the invertebrate ancestor. As in all other cases in this series of papers, when the facts of topographical anatomy, of morphology and embryology, all combine to the same conclusion as to the derivation of the vertebrate organ from that of the invertebrate, then there must be also a structural similarity between the two. What, then, is the nature of the coxal gland in the scorpions and *Limulus*? Lankester's paper gives us full information on this point as far as the scorpion and *Limulus* is concerned, and he shows that the coxal gland of *Limulus* differs markedly from that of *Scorpio* in the size of the cells and in the arrangement of the tubes. In fig. 20, A, I give a picture of a piece of the coxal gland of *Limulus* taken from Lankester's paper.<sup>2</sup>

Turning now to the vertebrate, Bela Haller's paper gives us a number of pictures of the glandular hypophysis from various vertebrates, and he especially points out the tubular nature of the gland, and its solidification in the course of development in some cases. In fig. 20, B, I give his picture<sup>3</sup> of the gland in *Ammocœtes*.

The striking likeness between Haller's picture and Lankester's picture is apparent on the face of it, and shows clearly that the histological structure of the glands in the two cases confirms the deductions drawn from the anatomical and morphological positions.

<sup>1</sup> *Op. cit.*

<sup>2</sup> "On the Skeleto-trophic Tissues and Coxal-glands of *Limulus*, *Scorpio* and *Mygale*," *Q. J. of Micr. Sci.*, fig. 1, Pl. X.

<sup>3</sup> *Op. cit.*, fig. 29, Taf. V.

The sequence of events which gave rise to the pituitary body of the vertebrate was in all probability somewhat as follows:—

Starting with the excretory glands of the Phyllopoda, known as shell glands, which existed almost certainly in the phyllopod Trilobite, we pass to the coxal glands of the Merostomata. Judging from *Limulus* these were co-extensive with the coxæ of the 2nd, 3rd, 4th, and 5th locomotor appendages. When

A

B

n. a.

FIG. 20, A.—Section of coxal gland of *Limulus* (from Lankester).

B.—Section of pituitary body of *Ammocoetes*. n. a., termination of nasal passage (from Bela Haller).

these appendages became reduced in size and purely tactile they were compressed and concentrated round the mouth region, forming the endognaths of the Merostomata; as a necessary consequence of the concentration of the coxæ of the endognaths the coxal gland also became concentrated, and took up a situation close against the pharynx, as represented in fig. 17, B. When then the old mouth closed and the pharynx became the saccus vasculosus, the coxal gland remained in close contact with the saccus vasculosus and became the pituitary body, thus giving the reason why there is always so close a connection between the pituitary body and the infundibular region.

#### *The Primordial Cranium.*

How did the old mouth close? Clearly, seeing that, as already mentioned, the olfactory tube was morphologically

quite independent of the mouth, it was an easy thing for something to grow between the mouth and this tube if the food no longer passed that way, especially if that something was at the time in vigorous growth and increasing in importance. This important factor in the change from the Eurypterid to the Vertebrate was clearly the tissue of the cranial wall, a tissue which at first, as seen in *Ammocoetes*, was of a peculiar character, neither fibrous connective tissue nor yet cartilage—a massive connective tissue, to use Lankester's phrase—which at transformation becomes cartilaginous, forming the cartilaginous cranium of *Petromyzon*. This cartilage is of the hard variety, continuous with that of the trabeculae and parachordals, and was formed in a gelatinous tissue like that of the plastron or entosternite, and not in a muco-cartilage like the soft cartilages. What, then, is the cranial wall? from what did it originate? Clearly it is simply the plastron itself, which has surrounded the vital organs of the brain and so formed an internal protecting cranium.

In Part II. of this series of papers I have discussed the formation of the trabeculae and come to the conclusion that they were formed from two lateral thickened bars of the plastron, which took up a position lateral and ventral to the brain mass, either because that was the original position, or because the lateral portions of the plastron have been pushed to one side owing to the growth of the infra- and supra-oesophageal brain mass. The conversion of the anterior part of the plastron into lateral trabeculae is well seen in *Galeodes*; as the figures 12 and 13 show, the anterior part of the plastron (*pl.*) is reduced to two lateral bars on each side of the brain mass, for no part of the infra-oesophageal ganglia lies ventral to the plastron, while the posterior part is formed by the junction of these two lateral bars in the middle line. Further, we see that two wings arise from these lateral trabeculae and pass directly dorsalwards, thus commencing to enclose a median chamber, which contains only the brain and the alimentary canal with its appendages; these wings give attachment to various muscles.

The same sort of arrangement is seen in *Phrynos*; here, too, the walls of the plastron form a primordial cranium.

As is seen in fig. 5, the plastron (*pl.*) forms a smooth cup, within which the supra-oesophageal ganglia and alimentary canal with its accessories are lying. In its front part it extends round the pharynx and close up to the mouth; at its lateral parts it approaches the inner surface of the dorsal wall of the carapace, and, as already mentioned, gives origin on each side to the tendons of the oblique muscle (*m. obl.*). To the external or outer surface are attached the sterno-coxal muscles of the appendages.

In every respect the front part of the cranium of *Ammocoetes* corresponds with this plastron, and it is instructive to see how the glandular tissue of the pituitary body is imbedded and mixed up with the tissue of this cranial wall, how the termination of the nasal tube is imbedded in this same thickened mass of the cranial wall—how, in fact, both coxal gland and olfactory tube have become involved in the growth of the tissue of the plastron by means of which the mouth was closed.

I speak only of the front part of the cranium. I have purposely throughout these papers kept silent on the subject of the parachordals and the auditory capsule; they will be considered when I come to deal with the auditory organ.

This is the reason why it has proved impossible for all morphologists to resolve the cranium into a series of segments because it was formed from the plastron, and the component segments of the plastron are far to seek.

## PART VII.—ON THE EVIDENCE OF PROSOMATIC APPENDAGES IN AMMOCETES, AS GIVEN BY THE COURSE AND DISTRIBUTION OF THE TRIGEMINAL NERVE.

This part of my paper consists largely of the tracing of the branches of the trigeminal nerve, of the origins and insertions of muscles, and of the position of the skeletal structures by means of serial sections through the head region of *Ammocoetes*, a task which has been carried out by Miss Alcock in the same way as in the previous paper by her on the distribution of the nerves of the branchial region, so that the facts recorded in this

part of my series of papers are very largely due to her. I have, however, thought better not to interrupt the sequence of my argument by putting in her work as a separate paper, and shall therefore continue to speak in the first person.

I have already, to a large extent, anticipated this part of my paper by the comparison of the diagrams on p. 524, in which an ideal section of a Eurypterid is compared with a section of the early or larval stage of the Ammocetes. This comparison implies that the oral chamber of Ammocetes arose from the accessory-oral or metastomal chamber of the Eurypterid, that therefore the lower lip of the Ammocetes originated from the last pair of prosomatic appendages or metastoma, which had fused in its basal part with the basal part of the opercular segment to form a septum between this oral chamber and the original branchio-genital chamber. We ought, therefore, to expect to find in Ammocetes evidence of a separate segment of the same nature as the branchial segments already discussed in Parts III. and IV., but not bearing branchiæ, immediately in front of and intimately connected with the thyroid segment. Such a segment would be innervated by a separate part of the trigeminal nerve; and its muscles would include the muscles of the septum in part as well as those of the lower lip.

The rest of the motor part of the trigeminal nerve supplies in Ammocetes the muscles of the tentacles and the upper lip; and, in accordance with the comparison indicated, arose from the conjoined prosomatic appendage nerves, which supplied originally the ectognaths and the endognaths, together with the endostoma or pro-mesosternite, to which the sterno-coxal processes of the latter were attached. Of these tentacles, it is suggested, from the comparison of the diagrams, that the large ventral tentacle, which is known to be formed by the fusion of the most ventral pair, called by Rathke the tongue, is the representative of the pair of ectognaths, while the rest of the tentacles represent the concentrated endognaths.

In this paper I propose to see how far the actual distribution of the nerves, the muscles, and the skeletal structures lend countenance to this suggestion.

The first fact which strikes one as very suggestive is that the structures innervated by the trigeminal in the Ammocetes are

extraordinarily different from those which it innervates in higher Vertebrates, and, indeed, in *Petromyzon* itself; for, just as the thyroid segment disappears at transformation, so the peculiar structures in the oral cavity of *Ammocoetes*, known as the tentacles and the velar folds, disappear at transformation, and give way to the tongue and suctorial apparatus of the adult animal. Such persistence in the larval condition with disappearance at transformation points strongly to the conclusion that in these organs, as in other cases, we have a clue to the pre-vertebrate condition of the ancestor of *Ammocoetes*.

The second suggestive fact is that all these structures, which I regard as having originally been prosomatic appendages, arise embryologically as outbuddings, much in the same way as they must do if they were derived from arthropod appendages.

Thus, undoubtedly, as described by Balfour, the tentacles all arise as distinct outgrowths, and so also does the lower lip. The oral chamber is usually spoken of as the stomodæum or stomodæal invagination, and the septum separating it from the respiratory chamber is called the septum of the stomodæum; it is acknowledged to differ from the stomodæum of other Vertebrates by its extensive length. Judging from Dohrn's and Kupffer's<sup>1</sup> description and illustrations, this chamber would be more truly described as formed, not by invagination, but by the forward growth of a ventral outgrowth or lower lip, which, as is seen from their illustrations, grows forward from the anterior limiting septum of the branchial chamber. Subsequently when the animal is 5 mm. in length a larval metamorphosis takes place according to Kupffer, characterised by a rapid forward growth of the upper lip, by which the nasal orifice is brought to the dorsal surface, and thus by the forward outgrowth of the upper and lower lips the deep large oral chamber of the *Ammocoetes* is formed.

The formation of the fused pair of appendages called the metastoma in the Eurypterids by which an accessory oral chamber was formed must have taken place by the forward growth of a ventral outbudding in much the same way as the lower lip of *Ammocoetes* is formed.

<sup>1</sup> Stud. z. vergleich. Entwickl. d. Kopf. d. Kranioten. 2<sup>te</sup> Heft. "Die Entwicklung des Kopfes von *Ammocoetes Planeri*." 1894.

*The Segment of the Lower Lip, or Metastomal Segment.*

We have seen that in the branchial or mesosomatic region the segments corresponding to the mesosomatic appendages were mapped out by means of their supporting or skeletal structures, their segmental muscles, and their nervous arrangements, as well as by the arrangement of the branchiæ. Similarly the segments in front of the branchial region corresponding to the prosomatic appendages ought to be definable by the same means, although, owing to the absence of branchiæ and the greater concentration in this region, the separate segments would probably not be so conspicuous.

The last segment considered in this series of papers was the segment belonging to the VIIth nerve corresponding to the opercular appendages of the Eurypterid. The segment immediately in front of this is the next for consideration, viz., that corresponding to the chilarial appendages or metastoma; and as the basal part of this pair of appendages was fused with the basal part of the operculum, the one cannot be discussed without the other; therefore the segment to which the lower lip belongs must be considered in connection with and not apart from the thyro-hyoid segments already dealt with.

In Part II. (*this Journ.*, vol. xxxii. p. 560) of this series of papers I stated, in anticipation of this present part, that the skeletal supporting structures of the foremost head segments were composed, not of cartilage as in the branchial region, but of muco-cartilage, and that the arrangement of these muco-cartilaginous plates and bars indicated the nature of the invertebrate segments in this region.

Just as each of the branchial segments is marked out by its separate cartilaginous bar, so the segments in front are characterised by their separate supporting muco-cartilaginous bars. It is of special interest, in connection with the segments indicated by such supporting structures, to find that this special tissue is entirely confined to the head region and disappears absolutely at transformation, thus indicating the ancestral nature of the segments marked out by its presence.

This muco-cartilaginous skeleton is the key to the whole posi-



tion, and requires, therefore, to be understood. It is of great importance, not only because it demonstrates the position of the segments in *Ammocoetes* which characterised its invertebrate ancestor, but also because it possesses a structure remarkably similar to that found in the head plates of the most ancient fishes. For the present I will confine myself to the consideration of this muco-cartilaginous skeleton as evidence of the relationship of *Ammocoetes* to the Eurypterids, and in Part VIII. will show how absolutely the same skeleton corresponds to that of the Cephalaspidæ, so that the *Ammocoetes* is really a slightly modified Cephalaspid, the larval form of which was Eurypterid in character.

In Part III. of this series of papers (*this Journ.*, vol. xxxiii. Pl. III. figs. 1 and 2) I have given a representation of the dorsal and ventral views of an *Ammocoetes* cut in half horizontally. Such a section shows with great clearness the series of branchial appendages with their segmental muscles and cartilaginous bars which form the branchial segments innervated by the IXth and Xth nerves according to my view of the branchial unit. As is seen in those figures, the skeletal bar of the hyoid or opercular appendage, which is clearly serially homologous with the other branchial bars, is composed of muco-cartilage and not of cartilage. If we follow this series of horizontal sections nearer to the origin of the cartilaginous bars from the sub-chordal cartilaginous rod on each side of the notochord, we obtain a picture as in fig. 1, Pl. LVI., in which each branchial segment is defined by the section of the branchial cartilaginous bar ( $sk_4, sk_5$ ), by the section of the separate branchiæ ( $br_2, br_3$ ), and by the separate segmental muscles arranged round each bar, which are partly ordinary striated ( $m_4, m_5$ ), partly tubular ( $mt_3, mt_4$ ). The uppermost of these branchial segments shows the same arrangement; ( $sk_3$ ) is the branchial skeletal bar, which is now composed of muco-cartilage, not cartilage; ( $br_1$ ) is the branchiæ in the same situation as the rest, but here composed of glandular rather than of respiratory epithelium, while the ordinary striated branchial muscles of this segment are marked as ( $m_3$ ), being separated from the tubular muscles of the segment ( $mt_2$ ), owing to the large size of the blood space in which these latter muscles are lying. In front of this segment so defined we see again another well-

marked skeletal bar ( $sk_2$ ) of muco-cartilage, evidently indicating a similar segment anterior to the hyoid segment. In connection with this bar there are no branchiæ, but again we see two sets of visceral muscles, the one ordinary striated, marked ( $m_2$ ), and the other tubular, marked ( $mt_1$ ). Here, then, the section indicates the existence of a segment of the same character as the posteriorly-situated branchial segments but belonging to a non-branchial region—a segment which would represent a non-branchial appendage, the last therefore of the prosomatic appendages. Let us, then, follow out these two segmental muco-cartilaginous bars and their attendant muscles, and see what sort of segments we thereby form.

The bar which comes first for consideration ( $sk_3$ ) arises immediately behind the auditory capsule from the first branchial cartilage very soon after it leaves the sub-chordal cartilaginous ligament; the soft cartilage of the sub-chordal ligament ceases abruptly to extend along the notochord at the place where the hard cartilage of the parachordal joins it, and in a sense it may be said to there leave the notochord and pass into the basal part of the first branchial bar. The most anterior continuation of this branchial system is this muco-cartilaginous bar ( $sk_3$ ), which passes forward and ventralwards, being separated from the axial line by the auditory capsule (*cf.* figs. A, B, C, Pl. LVII.). Its position is well seen in a sagittal section, such as fig. 12, Pl. LVI. It follows absolutely the line of the pseudo-branchial groove, and ventrally joins the plate of muco-cartilage which covers the thyroid gland. It forms a thickened border to this plate anteriorly, just as the branchial cartilaginous bars border it posteriorly. In fact, it behaves with respect to the hyoid segment in a manner similar to the rest of the cartilaginous bars with respect to their respective segments.

It represents, although composed of muco-cartilage, the cartilaginous bar of the operculum in *Limulus*, which also forms the termination of the branchial cartilaginous system, as fully explained in Part II. of this series of papers; it may therefore be called the opercular bar.

The next bar ( $sk_2$ , in fig. 1, Pl. LVI.) is extremely interesting, as we are now out of the branchial or mesosomatic region, and into the region corresponding to the prosoma. It starts from a

cartilaginous projection made of hard cartilage, just in front of the auditory capsule, called by Parker the pedicle of the pterygoid,—a projection (*ped* in fig. 1, Pl. LVI.) which defines the posterior limit of the trabeculæ on each side, where they join on to the parachordals,—and winding round and below the auditory capsule, joins the opercular bar (see Pl. LVII.), to then pass into and form part of the muco-cartilaginous plate of the lower lip. In the actual section figured, this projection of hard cartilage is not directly continuous with (*sk*<sub>2</sub>), owing to a slight curvature in the bar; the next few sections show clearly the connection between (*ped*) and (*sk*<sub>2</sub>), and consequently the complete separation by means of this bar of the hyoid segment from the segment in front. In the figures on Pls. LVI., LVII., the hard cartilage is coloured purple, the soft cartilage blue, and the muco-cartilage red, so that the position of this bar is well shown. This bar may be looked upon as bearing the same relation to the muco-cartilaginous plate of the lower lip as the opercular bar to the muco-cartilaginous plate over the thyroid; and seeing that these two plates form one continuous ventral head-shield of muco-cartilage (Pl. LVII., B), and also that this bar fuses with the opercular bar, we may conclude that the segment represented by the lower lip is closely connected with the hyoid or opercular segments. In other words, if the lower lip arose from the metastoma, then this pair of skeletal bars might be called the metastomal bars, which formed the supporting skeleton of the last pair of prosomatic appendages, and, as is likely enough, arose in connection with the posterior lateral horns of the plastron; these posterior lateral horns, like the rest of the plastron, would give rise to hard cartilage, and so form in *Ammocetes* the two lateral so-called pterygoid projections.

In the branchial region the muscles which marked out each branchial segment were of two kinds, ordinary striated visceral muscles and tubular muscles. Of these the former represented the dorso-ventral muscles of the branchial appendages, while the latter formed a separate group of dorso-ventral muscles with a separate innervation which may have been originally the segmental veno-pericardial muscles so characteristic of *Limulus* and the scorpions. In figs. 1, 2, Pl. LVI., the grouping of these muscles

in each branchial segment is well shown, and it is immediately seen that the hyoid segment possesses its group of striated visceral muscles ( $m_3$ ) supplied by the VIIth nerve in the same manner as the posterior groups, as has already been pointed out by Miss Alcock in her previous paper. Passing to the segment in front, fig. 1 shows that the group of visceral muscles ( $m_2$ ) would correspond in relative position with respect to the metastomal bar to the hyoid muscles with respect to the opercular bar or to the branchial visceral muscles with respect to each branchial bar. What, then, is this muscular group? The series of sections show that these are the dorso-ventral muscles belonging to the lower lip which, as seen in fig. 21, M, form a well-marked muscular sheet, the fibres of which interlace across the mid-ventral line of the lower lip. This group of lower lip muscles is very suggestive, for they arise, not from the trabeculae, but from the front dorsal region of the cranium, just in front of the two lateral eyes. In fig. 2, Pl. LVI., their dorsal part is seen cut across on its way to its dorsal attachment. Such an origin is reminiscent of the tergo-coxal group of muscles, arising, as they do, from the primordial cranium and the tergal carapace; and suggests at once that when the chilarial appendages expanded to form a metastoma, their tergo-coxal muscles formed a sheet of muscles similar to those of the lower lip of *Ammocoetes*, by which the movements of the metastoma were effected. The posterior limit of these muscles ventrally marks out the junction of the segment of the lower lip with that of the thyroid; in other words, indicates where the metastoma has fused ventrally with the operculum (fig. 2, Pl. LVI.).

Besides the striated visceral muscles, each branchial segment possesses its own tubular muscles, shown in fig. 2, Pl. LVI. ( $mt_3$ ) and ( $mt_4$ ). As the section shows, there is clearly a group of tubular muscle fibres belonging to the hyoid segment ( $mt_2$ ), and also another group belonging to the segment in front of the hyoid ( $mt_1$ ); so that, judging from this section, each of these segments possesses its own tubular musculature just as the branchial segments, the difference being that the tubular muscles are more separated from the striated visceral group than in the true branchial segments, owing to the size of the blood spaces surrounding them. What, then, are these two groups of muscles?

Tracing them in the series of sections, both groups are seen to belong to the system of velar muscles, forming an anterior and a posterior group respectively; and we see, further, that there is not the slightest trace of any tubular muscles anterior to these muscles of the velum.

In the living *Ammocoetes* the velar folds on each side can be seen to move synchronously with the movements of respiration,

M

Th

FIG. 21.—Ventral view of head region of *Ammocoetes*. Th, thyroid gland; M, lower lip with its muscles.

contracting at each expiration and thus closing the slit by which the oral and respiratory chambers communicate, and so forcing the waters of respiration through the gill slits, as described by Schneider. Such a fact is clear evidence that these

tubular muscles of the velar folds belong to the same series as the tubular muscles of the branchial segments, so that if, as I have already suggested, the latter muscles were originally the veno-pericardial muscles of segments corresponding to the branchial appendages, then the former would represent the veno-pericardial muscles of the segments corresponding to the opercular and metastomal appendages. What, then, are these velar folds, and how is it that the tubular muscles of these two segments become the velar muscles? I will consider, in the first instance, the posterior group of muscles ( $mt_2$ ) in fig. 1, Pl. LVI.

It has already been pointed out that the tubular muscles of the branchial segments are dorso-ventral, but do not run with the ordinary constrictors, having separate attachments and running part of their course internal to and partly external to the ordinary constrictors. At first sight, as is usually stated, the hyoid segment does not appear to possess tubular muscles at all. If, however, we follow the posterior group of velar muscles ( $mt_2$ ), we see (fig. 2, Pl. LVI.) that they pass between the auditory capsule and the opercular bar ( $sk_3$ ) of muco-cartilage to reach the region of the jugular vein ( $j.v.$ ) posterior to the auditory capsule, so that their dorsal origin bears the same relation to the hyoid segment as the dorsal attachment of the rest of the tubular muscles to their respective segments. Further, these muscles run along the length of the velar fold, and are attached ventrally on each side of the thyroid gland, so that their ventral attachment also corresponds in position as regards the hyoid segment with the ventral attachment of the rest of the tubular muscles as regards their respective segments.

This ventral attachment is shown in fig. 21 on each side of the thyroid and in fig. 22; while in fig. 2, Pl. LVI., the fibres are seen converging to this ventral position. In other words, this large posterior muscle of the velar folds is a dorso-ventral muscle, and would actually take the same position in the hyoid segment as the dorso-ventral tubular muscles in the other branchial segments, if the velum were put back into its original position as the septum terminating the branchial chamber. Conversely, the presence of these hyoid tubular muscles in the velum gives evidence that the opercular segment takes part in the formation of the septum, as already suggested.

Miss Alcock, in her paper,<sup>1</sup> speaks of tubular muscles belonging to the hyoid segment, which are attached to the muco-cartilage. Schaffer<sup>2</sup> also speaks of certain tubular muscles belonging to the velar group as piercing the muco-cartilage (*h r s*) in his figures 24 and 25, *i.e.*, the metastomal bar, near its junction with the opercular bar. In my specimens there is a distinct group of tubular muscles which pierce the opercular bar of muco-cartilage at its junction with the metastomal bar, and pass into the posterior group of velar muscles. They clearly belong to the hyoid segment, as Miss Alcock supposed, but are not attached to the muco-cartilage. It is possible that they represent a different group to those already considered, and suggest the possibility that this opercular or thyro-hyoid segment is double with respect to its original veno-pericardial muscles as well as in other respects.

The anterior group of tubular muscles (*mt*<sub>1</sub>, figs. 1, 2, Pl. LVI.) belonging to the same segment as the metastomal bar must be now taken into consideration. Very different is their origin to that of the posterior group: they arise close up against the eye, and have given risen to Kupffer's and Hatschek's confusion that the superior oblique muscle of the eye arises from a part of the velar musculature. Naturally, as Neal<sup>3</sup> has pointed out, they have nothing to do with the eye muscles; the superior oblique muscle is plainly in its true place apart entirely from these velar muscles, which form the foremost group of the segmental tubular muscles. They pass into the anterior part of the velar folds and run round to the ventral side just in the same way as the posterior group. This muscle represents the veno-pericardial muscle of the segment immediately in front of the opercular, *i.e.*, the metastomal segment, and is the foremost of these veno-pericardial muscles. Its presence shows that the velar folds, formed as they were by the breaking down of the septum, are in reality part of two segments, *viz.*, the opercular and the metastomal, which have fused together in their basal

<sup>1</sup> R. Alcock, "The peripheral distribution of the cranial nerves of *Ammocætes*," *this Journal*, vol. xxiii. p. 141, 1898.

<sup>2</sup> Schaffer, "Ueber d. Knorpelige Skelett v. *Ammocætes*," &c., *Zeitsch. f. Wiss. Zool.*, vol. lxi. p. 635, 1896.

<sup>3</sup> *Op. cit.* See discussion of Hatschek's and Kupffer's views on the origin of the eye muscles, pp. 192, 193, 204, 205.

parts, and by such fusion have caused the inter-relationship between the VIIth and Vth nerves, so apparent in the anatomy of the vertebrate cranial nerves.

The existence of a veno-pericardial muscle in a segment in front of the mesosomatic region is highly probable, seeing that Benham in his description of the veno-pericardial musculature of *Limulus* says,<sup>1</sup> "Besides the six pairs in the abdomen two pairs occur on each side of the thoracic entochondrite." (See Part iii. p. 172, fig. 5, *vp.*)

Again, the supposition that the segmental tubular muscles belong throughout to the veno-pericardial group, gives an adequate reason why they do not occur in front of the velum; for as their existence is dependent upon the longitudinal collecting sinus in *Limulus* and the scorpion, which is represented by the ventral aorta in *Ammocoetes*, they cannot extend beyond its limits. Now Dohrn<sup>2</sup> asserts that the ventral aorta terminates in the spiracular artery, which exists only for a short time; and in another place, speaking of this same termination of the ventral aorta, he states<sup>3</sup>: "Dass je eine vorderste Arterie aus den beiden primären Aesten des Conus arteriosus hervorgeht, die erste Anlage der Thyroidea umfasst, in der Mesodermfalte des späteren Velums in die Höhe steigt um in die Aorta der betreffenden Seite einzumünden." These observations show that the vessel which in *Ammocoetes* represents the longitudinal collecting sinus in the Merostomata does not extend further forwards than the velum, and in consequence the representatives of the veno-pericardial muscles cannot extend into the segments anterior to the velum. One of the extraordinary characteristics of these tubular muscles which distinguish them from other muscles but brings them into close relationship with the veno-pericardial group is the manner in which the bundles of muscle fibres are always found lying freely in a blood space; this is clearly seen in the branchial region, but most strikingly in the velum, the interior of which, apart from its muco-cartilage, is simply a large lacunar blood space traversed by these tubular muscles. Such blood spaces are very striking from the point of view

<sup>1</sup> *Op. cit.*, p. 331.

<sup>2</sup> A. Dohrn, *Mitth., a. d. Zool. Stat. Neapel*, fig. 4, Pl. X., vol. 8, xiii. Stud.

<sup>3</sup> *Ibid.*, p. 253.



of this series of papers, but cannot be considered here; I shall therefore leave the discussion of their meaning to the part which will deal with the origin of the vascular and lymphatic systems of the Vertebrate.

The consideration of the tubular muscles of the velum leads distinctly to the conclusion that the velum belongs to two segments, the posterior part belonging to the hyoid or opercular segment, and the anterior part to the segment immediately in front of the hyoid. This latter segment ought, according to the theory, to have been the metastomal segment, and consequently the anterior portion of the velum ought to bear some distinct relation to the lower lip. In striking confirmation of such relation is the course of the nerve which supplies the muscles of the lower lip.

In fig. 5, Pl. LVI., the distribution of the trigeminal nerve is given, its motor branches being coloured red. The most posterior branch containing motor fibres is the large conspicuous nerve called by Hatschek<sup>1</sup> and others the mandibular or velar nerve. It arises so separately from the rest of the trigeminal as almost to deserve the title of a separate nerve. When it leaves the large posterior ganglion of the trigeminal it passes into the anterior part of the velum close alongside the anterior group of tubular muscles already spoken of. In its origin, therefore, it represents the nerve belonging to the same segment as the anterior tubular muscles. It passes into the velum, runs along with the tubular muscles to the ventral surface as far as the junction of the lower lip with the thyroid plate, and has not been followed further by Hatschek. Here, instead of passing backward with the tubular muscles, it bends abruptly forwards to supply the lower lip. In my address at Liverpool I spoke of the termination of this nerve in the median ventral tentacle or tongue. This was a mistake; Miss Alcock has traced it to its destination, and proved that it terminates in the muscles of the lower lip. The segmental nerve, then, of the anterior portion of the velum is the motor nerve of the lower lip, and we see that this nerve and the thyroid branch of the facial behave with respect to the lower

<sup>1</sup> Hatschek, "Ueber die Metamerie des Wirbelthier Kopfes," *Anat. Anzeiger*, 1892.

lip and the thyroid segment in precisely the same manner as the metastomal nerve and genital branch of the opercular nerve behave with respect to the metastoma and operculum respectively. (See fig. 17.)

Further, in the velum itself this nerve supplies an ordinary striated muscle belonging to the metastomal segment. This muscle is the only non-tubular muscle belonging to the velum; it is the muscle by which the anterior portion of the velar folds are drawn apart from each other and so the slit opened through which the food and mud must pass. This muscle is attached laterally to the muco-cartilage of the metastomal bar ( $sk_2$ ) at its junction with the muco-cartilage of the lower lip, and spreads out into a number of strands which are attached at intervals along the whole length of the free anterior edge of the velum. It represents a metastomal muscle not belonging to the tergo-coxal group, and is seen in section in fig. 2, Pl. LVI.

As to the innervation of the tubular muscles, the anterior group is certainly supplied by the velar nerve, and apparently so also is the posterior group. Considering the peculiarity of the nerve supply of these tubular muscles by a special nerve, the *profundus branchialis* of the VIIth nerve, I fully expected to find a branch of the *profundus branchialis* passing off with these tubular muscles at their origin behind the auditory capsule. Neither Miss Alcock nor I myself have succeeded in finding such a branch. On the other hand, she has been unable to find any difference in the innervation of the two groups of tubular muscles; the velar nerve supplies both. I conclude, therefore, that the separate system of nerves which innervates the tubular muscles arises at the junction of the prosomatic and mesosomatic system of nerves and runs to the foremost tubular muscles in conjunction with the last prosomatic nerve. The whole question of the origin of this system cannot be adequately discussed until we know the origin of the nerves which supply the heart and veno-pericardial muscles in *Limulus*.

Both parts of these velar folds possess a supporting skeleton of muco-cartilage; that in the opercular part of the velum follows the opercular bar or the pseudo-branchial groove from

the dorsal to the ventral surface. It affords, in connection with the opercular bar, yet another indication of the double nature of the hyoid or opercular segment.

The anterior portion is attached dorsally near the middle line on each side at the level of the so-called pedicle of the pterygoid, and possesses a wedge of muco-cartilage at its attachment, which arises from the trabeculae immediately in front of the pedicle, close to the place where the metastomal nerve and the anterior tubular muscles enter. It forms that part of the velar folds which come together in the middle line



FIG. 22.—*Ammocetes* cut open in mid-ventral line to show position of velum; velar folds removed on one side. *tr*, trabecula; *vel*, velum; *B*, anterior gnathic portion of velum; *pa.br.*, pseudo-branchial groove; *m<sub>2</sub>*, muscles of lower lip segment; *m<sub>3</sub>*, muscles of thyroid segment; *mt<sub>2</sub>*, insertion of tubular muscles of velum near thyroid.

and close the entrance into the respiratory chamber. As is seen in fig. 22, *B*, and was attempted to be shown in fig. 2 *ser*, Pl. III., Part III., this most dorsal anterior portion forms a somewhat separate well-defined rounded basal projection, the surface of which is most striking and suggestive, for it is markedly serrated, being covered over with a large number of closely-set projections or serræ. The serration of the surface here is of so marked a character that Langerhaus<sup>1</sup> considered this part of the velar folds to act as a masticating organ, grinding and

<sup>1</sup> P. Langerhaus, "Untersuchungen über *Petromyzon planeri*," *Bericht. v. d. Verhandl. d. Naturf., Gesellschaft z. Freiburg*, 1873.

rasping the food and mud which passed through this narrow slit. In fact, Langerhans supposed that this portion of the velum acted in a manner closely resembling the action of the gnathobases of the prosomatic appendages in *Limulus* or the Eurypterida. In addition to this marked serrated edge the whole surface of this anterior portion of the velum is covered over with a scale-like or tubercular pattern remarkably like the surface ornamentation seen in many of the scorpion group or the ancient Eurypterida. In fig. 23 I give a picture of this surface-marking of the velum. It is striking to see that just as in the case of the invertebrate this marking and these

FIG. 23.—Surface view of anterior surface of velum.

serræ are formed simply by the cuticular surface of the epithelial cells; a surface which, according to Wolff, contains chitin. The interpretation which I would give of the velar folds is therefore as follows:—

They represent the fused basal parts of the opercular and metastomal appendages, the gnathobases of the latter still retaining in a reduced degree their rasping surfaces, because, owing to their position on each side of the opening into the respiratory chamber, they were still able to manipulate the food as it passed by them after the closure of the old mouth.

#### *The Tentacular Segments.*

In front of this segment of the lower lip or metastoma, fig. 1, Pl. LVI., shows yet again a bar of muco-cartilage ( $sk_1$ ), dividing off another segment or segments, which arises, as in the other cases, from the axial cartilaginous skeleton; also striated muscles ( $m_1$ ), belonging to the visceral group which are innervated by the trigeminal nerve, but, as already explained, no tubular muscles. In accordance, therefore, with the interpretation already given, these bars and these muscles must indicate

segments of the nature of appendages in front of the metastomal segment. Starting, as in all cases, with the skeletal elements, we find (Pl. LVII.) that a pair of large bars of muco-cartilage ( $sk_1$ ) start from the termination of the trabeculae, and pass ventrally to fuse with the muco-cartilaginous plate of the lower lip (fig. 2, Pl. LVI.). This large bar forms the tentacular ridge on each side, and gives small projections of muco-cartilage into each tentacle. In addition to this tentacular bar, a special bar of muco-cartilage exists for the fused pair of median tentacles, the so-called tongue, which extends in the middle line along the whole length of the lower lip, being separated from the muco-cartilaginous plate of the lower lip by the muscles of the lower lip. This tongue bar of muco-cartilage joins with the muco-cartilage of the lower lip at its junction with the thyroid plate, and also with the tentacular bar just before the latter joins the muco-cartilaginous plate of the lower lip. This arrangement of the skeletal tissue suggests that the pair of tentacles known as the tongue stand in a category apart from the rest of the tentacles; a suggestion which is strongly confirmed by the separate character of its nerve supply, for (fig. 5, Pl. LVI.) a separate branch leaves the main motor nerve trunk to supply the tongue, while the rest of the tentacles are supplied by the main branch to the upper lip.

In fig. 5, Pl. LVI., Miss Alcock has drawn the distribution of the trigeminal nerve as traced by her through a series of sections; it arises, as is well known, from two separate ganglia, of which the foremost gives rise to a purely cutaneous nerve, the ophthalmic nerve, and the hindmost to three nerves, the most posterior of which is purely cutaneous, and passes tailwards over the ventral branchial region, as shown in the figure; the other two nerves, both of which contain motor fibres, are called by Hatschek the mandibular and maxillary nerves. Of these the former (*met*) has been considered; the latter, the maxillary nerve, which constitutes the large portion of the trigeminal, passes forwards from the ganglion, and at a point somewhere about the anterior region of the eyeball, divides into two, an external and an internal nerve. The external branch is apparently entirely sensory, and supplies the external surfaces of the upper and lower lips. The internal branch is mainly motor, and supplies

the muscles of the upper lip; it contains also the sensory nerves of the tentacles.

The nerve to the median ventral tentacle (*t*) or tongue leaves the internal division of the maxillary immediately after its separation from the external; it runs ventralwards, and at the same time passes internally till it reaches a position between the muco-cartilage and the epithelium lining the cavity of the throat. It then turns, and passing posteriorly (towards the tail) to the point where the median ventral tentacle is attached to the lower lip, it supplies some very rudimentary looking muscles which run from the tentacle to the adjoining surface, and no doubt serve to move the tentacle from side to side. A portion of the nerve still continues to run along the side of the median ventral ridge, as far back as the point where the muscles of the hyoid segment pass round the ventral side between the velum and the thyroid; in fact this small nerve passes along the whole length of the median ventral ridge.

This description shows that the trigeminal nerve divides itself into two groups: the one represented grey in the figure, which is purely cutaneous and sensory, corresponding, in the main, according to the theory, to the epimeral nerves of *Limulus*; the other coloured red and blue, which supplies muscles belonging to the visceral or splanchnic muscle group, and contains also the sensory nerves (blue) to the tentacles.

This latter group, which is formed by two distinct well-defined nerves, viz., the mandibular and the internal branch of the maxillary, corresponds, according to the theory, to the amalgamated nerves of the prosomatic appendages, and is clearly divisible into three distinct nerves:—

1. The lower lip nerve or the metastomal nerve (*met*).
2. The tongue nerve (*t*).
3. The nerve (*tent*) to the upper lip and tentacles.

Of these three pairs of nerves the first pair have been considered and reasons given why they may be looked upon as derived from the nerve to the metastomal appendage. The second pair of nerves ought, on this theory, to have originally supplied the pair of appendages immediately in front of the metastoma—that is, the pair of ectognaths, and therefore the ventral pair of tentacles known as the tongue would represent

the last remnant of these ectognaths. Similarly the other tentacles would represent the endognaths, and therefore the third pair of nerves would represent the fused nerves to these concentrated endognaths, which in the Eurypterids stand aloof from the ectognaths.

As we see, this method of interpretation attributes segmental value to the tentacles, a conclusion which is opposed to the general opinion of morphologists, who regard them as having no special morphological importance, and certainly no segmental value. On the other hand, the importance of the pair of ventral tentacles, the tongue of Rathke, which lie in the mid line of the lower lip, has been shown by Kaensche, Bujor, and others, all of whom are unanimous in asserting that at transformation they are converted into that large and important organ the piston or tongue of the adult *Petromyzon*. It is supposed that the rest of the tentacles vanish at transformation, being absorbed; they appear to me rather to take part in the formation of the sucking disc, so that I am strongly inclined to believe that the whole of the remarkable suctorial apparatus of *Petromyzon* is derived from the tentacles of *Ammocoetes*; in other words, on my view, a conversion of the prosomatic appendages into a suctorial apparatus takes place at transformation, just as is frequently the case among the Arthropoda.

Naturally we might expect to find evidence as to the segmental value of the tentacles in the arrangement of their muscles; Miss Alcock has, however, been unable to differentiate any special musculature for the tentacles apart from that of the upper and lower lips, with the exception of the rudimentary-looking muscles belonging to the median ventral tentacle, already mentioned; at the same time, it must be remembered that at transformation a very marked tongue musculature, innervated by the trigeminal nerve, makes its appearance and also the large muscles of the suctorial apparatus. These muscles may very possibly represent the intrinsic muscles of the tentacles; and until we know what represents them in the *Ammocoetes* stage, it is impossible to speak definitely upon the musculature of the tentacles. I feel strongly myself that the arguments I am able to bring forward in favour of the conversion of the endognaths and ectognaths into the tentacles of the

Ammocoetes are not as cogent and convincing as those dealing with the conversion of the metastomal, opercular, and branchial appendages, and I feel that it is necessary to know more about what takes place at transformation before it is possible to judge accurately of the morphological value of the tentacles. On the other hand, the discovery of Rohon mentioned on page 580, points to the existence in the old Cephalaspids of appendages presumably tentacular in nature which were more pronounced than in Ammocoetes.

Another difficulty with respect to the tentacles is the determination of the number of them, owing to the fact that in addition to what may be called well-defined tentacles a large number of smaller tactile projections are found on the surface of the upper lip, as is seen in fig. 2, Pl. III., Part III. In the very young condition 7 or 8 mm. in length it is easier to make sure on this point. At this stage they may be spoken of as arranged in two groups: an anterior small group and a posterior larger group. The anterior group consists of a pair of very small tentacles and a very small median tentacle, all three situated quite dorsally in the front part of the upper lip; the posterior group, which is separate from the anterior, consists of five pairs of much larger tentacles, the most ventral pair in the mid line ventrally on the lower lip being fused together to form the large ventral median tentacle or tongue already mentioned. This pair, according to Shipley, is markedly larger than the others. There are, therefore, five conspicuous tentacles on each side, and in front of them a smaller pair and a small median dorsal one. In the very young condition the accessory projections above-mentioned are not present, or at all events are not conspicuous, and also the tentacles are markedly larger in comparison to the size of the animal than in the older condition, where they have distinctly dwindled.

As shown in the comparison of the sections (fig. 17) the upper lip, in my opinion, is the pro-mesosternite, or endostoma, of the Eurypterid; it is therefore instructive to point out the change in the relation of the prosomatic appendages to this anterior sternal plate which has taken place in the Merostomata, a change which leads directly, in my opinion, to the position and innervation of the tentacles in Ammocoetes. We see,



According to Beecher's researches, that the gnathobases or sterno-coxal processes of the appendages in the Trilobites are arranged on each side of the middle line extending along the whole length of the animal. In *Limulus* (fig. 1) they are confined to the prosomatic region and form a distinct line of attachment to the anterior sternal plate along each side of the mid line around and posterior to the mouth orifice. Here we see also that although considerably concentrated the nerves to these appendages arise from the nervous system quite separately. In *Eurypterus* (fig. 3), as Helm has shown, the sterno-coxal processes of the 2nd, 3rd, 4th, 5th pairs of prosomatic appendages or endognaths are still more concentrated round the olfactory passage to the mouth, and, as we have noticed, the appendages themselves dwindle considerably, their main function being masticatory and tactile, so that a further stage of the same process, combined with the closure of the mouth orifice and consequent abolition of the masticatory function, would lead to four rudimentary tactile appendages or tentacles projecting from the anterior sternal plate or upper lip on each side of the mid-dorsal line just as in *Ammocoetes*. Owing to their concentration and dwindling of size they would be no longer innervated by four separate nerves but by a single tentacular nerve with four branches, as described by Hatschek and represented in fig. 5, Pl. LVI. Another suggestive fact with respect to the possible meaning of the tentacles is found in *Phrynos* and allied genera in the shape of tactile tentacular projections on the promesosternite. Fig. 24 represents the appearance of these. The median projection (A) is most striking, and is of special interest, as it forms the striker of a stridulating apparatus situated on the sterno-coxal process of each of the pedipalps; this organ will be especially dealt with in Part IX. of this series of papers dealing with the organ of hearing. Seeing that such tactile projections do exist on the promesosternite of this group of animals, it is easy to imagine that the mid-dorsal tentacle of *Ammocoetes* and those of the upper lip itself may have arisen as similar structures.

Finally, the pair of mid-ventral tentacles, called by Rathke the tongue, which are fused together and attached to the mid line of the lower lip, represents, according to the scheme, the

6th pair of prosomatic appendages; *i.e.*, in the Eurypterids the pair of large swimming appendages or ectognaths. Clearly, as figs. 2 and 3 show, they stand apart from the rest of the reduced prosomatic appendages in many instances; and as Holm has shown, their coxal joints fill in the lateral space between the metastoma and the endostoma, so that their bases are attached to the metastoma as well as the endostoma. In *Ammocoetes* they also stand apart from the rest in that they are larger and are attached to the mid line of the lower lip, are innervated by a branch of the trigeminal separate to that which supplies the rest of the tentacles, and on transformation become converted

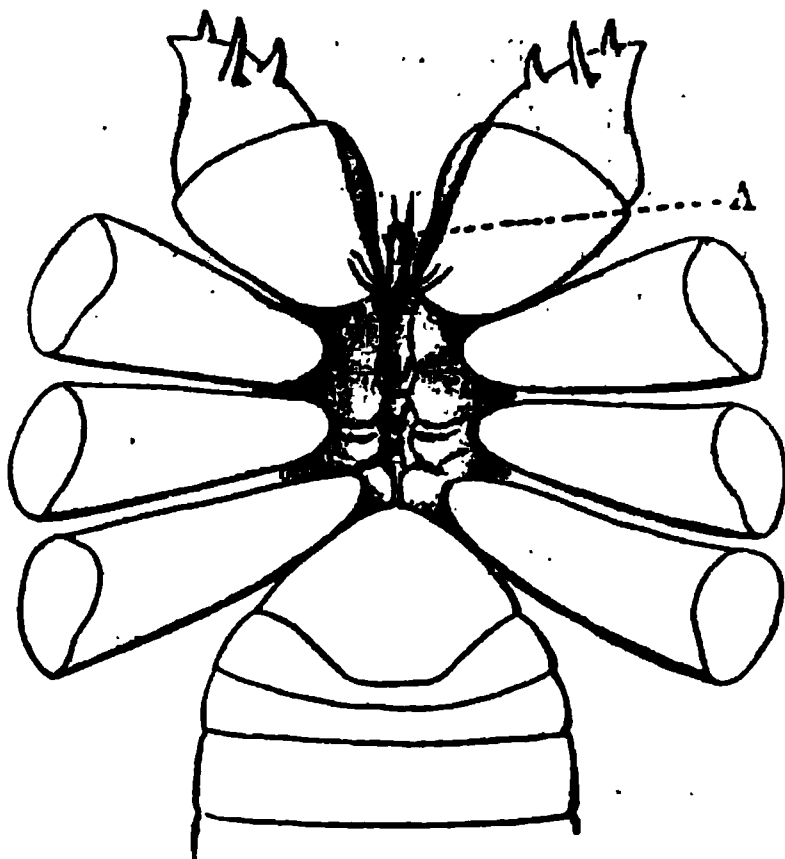


FIG. 24.—*Phrynos*, ventral surface. A, striker of stridulating organ.

into the tongue. In view of the suggestion that the tongue represents the ectognaths, and the rest of the tentacles the four endognaths, it is of great interest to draw attention to the uniform manner in which the concentration of the endognathal segments and the separateness of the ectognathal segment is marked out by all the separate factors which compose a segment in *Ammocoetes*; in all cases a concentration of four constituents followed by a single one. We may represent this in the following table.

To sum up, this part of the study of *Ammocoetes* shows that the whole front part of the head can be mapped out into segments

| V. Wijhe's<br>Segments. | Eurypterid<br>Segments. | Appendages.  |             | Appendage<br>Nerves.           | Skeletal<br>Elements.                 | Somatic<br>Motor Nerves.               | Dorso-<br>ventral<br>Segmental<br>Muscles.   | Coelomic<br>Cavities.               | Coxal<br>Glands.                                     |
|-------------------------|-------------------------|--------------|-------------|--------------------------------|---------------------------------------|--|--|-------------------------------------|--|
|                         |                         | Eurypterid.  | Ammocoetes. |                                |                                       |  |  |                                     |  |
| 1                       | 2<br>3<br>4<br>5        | 4 Endognaths | 4 Tentacles | 1 Tentacular<br>to 4 tentacles | 1 Tentacular<br>bar to<br>4 Tentacles | 1 Oculomotor<br>supplying<br>4 muscles | Sup. Inf. Int.<br>rectus and<br>Inf. oblique | 1 Preman-<br>dibular<br>fusion of 4 | 1 Pituitary<br>body; fusion<br>of 4 coxal<br>glands. |
|                         |                         | 1 Ectognath. | 1 Tongue.   | 1 Tongue<br>nerve.             | 1 Tongue bar                          | 1 Trochlearis<br>supplying<br>1 muscle | Sup. oblique                                 | 1 Mandibular                        |  |

serially homologous with those in the branchial region, if the segmental branchial unit be looked upon as a branchial appendage and not as a gill pouch. Such mapping out confirms the conclusions already arrived at, that the trigeminal nerve was originally not a single nerve, but, as far as the splanchnic part is concerned, was made up of the nerves to the prosomatic appendages, and that at the time when the old mouth was closed an accessory oral chamber already existed owing to the presence of the metastoma; this chamber was finally put into communication with the branchial chamber by the breaking down of the basal part of the conjoined metastoma and operculum, which formed a septum between the prosomatic chamber and the branchio-genital chamber described in Part IV. of this series of papers. We may conclude that in some such method the communication was effected phylogenetically, because such a breaking down of the septum does actually occur in the ontogeny.

As this Part VII. of this series of papers concludes the discussion of the meaning of all the segmental cranial nerves with the exception of the VIIIth, the nature of which I will consider in a separate part, it will be convenient here to redeem my promise given in Part II., and by means of a table show what, in my opinion, is the segmental position of the glossopharyngeal nerve. (See next page.)

I have also stated that in every part of this discussion I will consider whether my theoretical conclusions are in accordance with the six principles laid down in Part I. In the course of the discussion given in Parts III., IV., V., VI., and VII., I have already incidentally taken these principles more or less into consideration. I propose, however, after the auditory and optic nerves have been discussed, to sum up, in the light of these six principles, my views of the origin of the cranial nerves as a whole.

TABLE OF COMPARISON OF CORRESPONDING SEGMENTS IN THE EURYPTERIDS AND IN 'AMMOCEUTES  
(i.e., IN CEPHALASPIDS).

| Intra-oesophageal. |               | Proesophageal. |               |  |  |   |                                |                           |                                  |                            |                 | Mesoesophageal.    |                     |  |  |  |  |  |  |  |  |
|--------------------|---------------|----------------|---------------|--|--|---|--------------------------------|---------------------------|----------------------------------|----------------------------|-----------------|--------------------|---------------------|--|--|--|--|--|--|--|--|
| 3                  | 2nd           | "              | 4 Endognathus |  |  | 2 | Ventral part forms coral gland | 4 tentacles and upper lip | V Tentacular and upper lip nerve | Somatic Segmental Muscles. | Somatic Nerves. | Coelomic Cavities. | V Wijbe's Segments. |  |  |  |  |  |  |  |  |
| 4                  | 3rd           | "              |               |  |  |   |                                | Tongue                    | V Tongue nerve                   | Sup. oblique               | IV              | Mandibular         | 2                   |  |  |  |  |  |  |  |  |
| 6                  | 4th           | "              |               |  |  |   |                                | Lower lip                 | V Lower lip nerve                | Retractor bulbi (?)        | VI (?)          | Mandibular         |                     |  |  |  |  |  |  |  |  |
| 6                  | 5th           | "              | Ectognath     |  |  | 3 |                                |                           |                                  |                            |                 |                    | 3                   |  |  |  |  |  |  |  |  |
| 7                  | Chilaria      |                | Metastoma     |  |  | 4 |                                | Thyroid                   | VII                              | External rectus            | VI              | Hyoid <sub>1</sub> |                     |  |  |  |  |  |  |  |  |
| 8                  | Operculum     |                | Genital       |  |  | 5 |                                | Hyoid or 1st Branchial    |                                  |                            |                 | Hyoid <sub>2</sub> | 4                   |  |  |  |  |  |  |  |  |
| 9                  | 1st Branchial |                | Branchial     |  |  | 6 |                                | 2nd Branchial             | IX                               | ...                        | ...             | 2nd Branchial      | 5                   |  |  |  |  |  |  |  |  |
| 10                 | 2nd           | "              | 2nd Branchial |  |  | 7 |                                |                           |                                  |                            |                 |                    |                     |  |  |  |  |  |  |  |  |

| Vertebrate (Ammocoetes or Cephalaspids). |  |  |  |  |               |  |  |  |  |
|--|--|--|--|--|---------------|--|--|--|--|
| Pineal Eye.                              |  |  |  |  | Pineal Nerve. |  |  |  |  |
| Lateral Eye.                             |  |  |  |  | II            |  |  |  |  |
| Olfactory Organ.                         |  |  |  |  | I             |  |  |  |  |

| Supra-Infundibular. |  |  |  |  |  |  |  |  |  |
|---------------------|--|--|--|--|--|--|--|--|--|
|                     |  |  |  |  |  |  |  |  |  |
|                     |  |  |  |  |  |  |  |  |  |

## PART VIII.—THE PALÆONTOLOGICAL EVIDENCE: AMMOCOETES A CEPHALASPID.

So much for the evidence of prosomatic appendages in Ammocoetes, the skeletal supports of which were in connection with the axial skeleton, *i.e.*, with the trabeculæ and parachordals. With the consideration of these cartilaginous and muco-cartilaginous plates and bars, our search after primitive skeletal structures in Ammocoetes does not terminate, for Ammocoetes possesses in addition a plate of muco-cartilage over the head region, which, together with the ventral lower lip and thyroid plates, forms a skeletal covering to the front part of the head. This external muco-cartilaginous covering of Ammocoetes, which, in contradistinction to the ordinary vertebrate skeleton, may be spoken of as an external skeleton, is of the utmost importance, for, as we shall see, it represents the last trace of the external skeletal head covering so characteristic of the earliest fishes.

As already mentioned in Part II.<sup>1</sup> of this series of papers, I sent in an account of the distribution of the plates of muco-cartilage in Ammocoetes to the *Quarterly Journal of Microscopical Science* in 1895—which was never published—an account which was confirmatory of the work of Schneider and Kaensche, and was absolutely in agreement with the more elaborate paper of Schaffer<sup>2</sup> published in 1896. In addition, however, to the well-known plates of muco-cartilage which form ventrally the plate over the lower lip and thyroid (Schaffer's Mundrachenhöhlenplatte), and dorsally the plate of the upper lip, I gave my reasons in that paper why I considered that the whole branchial region was originally covered with dorsal and ventral plates of muco-cartilage, except along the lateral groove which contains the gill slits. The evidence is as follows:—

The somatic muscles of Ammocoetes form a continuous longitudinal sheet of muscles along the length of the body, which are divided up by connective-tissue bands into a series of imperfect segments or myotomes; this simple muscular sheet can be separated off along the whole of the head region of the animal, with

<sup>1</sup> *This Journal*, vol. xxxii. pp. 559–561.

<sup>2</sup> *Zeitschrift f. wissens. Zool.*, Bd. 61, 1896, p. 606.

the exception of the most anterior part, without interfering with the attachments or arrangements of the splanchnic muscular system in the least. The reason why this separation can be so easily effected is to be found in the fact that the two sets of muscles are not attached to the same fascia. The sheet of fascia to which the somatic muscles are attached is separated from the fascia which encloses the branchial cavity by a space (see Pl. III. in Part III.) filled with blood-spaces and cells containing fat, in which space is also situated the cartilaginous branchial basket-work. These branchial bars are closely connected with the branchial sheet of fascia, and have no connection with the somatic fascia, their perichondrium forming part of the former sheet. Upon examination, this space is seen to be mainly vascular, the blood spaces being large and frequently marked with pigment; but it also possesses a tissue of its own, recognised as fat tissue by all observers. The peculiarity of the cells of this tissue is their arrangement; they are elongated cells arranged at right angles to the plates of fascia, just as the fibres of the muco-cartilage are largely arranged at right angles to their limiting plates of perichondrium. These cells do not necessarily contain fat; and when they do, the fat is found in the centre of each cell, and does not push the protoplasm of the cell to the periphery, as in ordinary fat cells.

In fig. 25, B, I give a specimen of this tissue stained by osmic acid; in fig. 25, A, I give a drawing of ordinary muco-cartilage taken from the plate of the lower lip; and in fig. 26, A, a modification of the muco-cartilage taken from the velum, which shows the formation of a tissue intermediate between ordinary muco-cartilage and this branchial fat tissue.

Further, in fully-grown specimens of *Ammocoetes*, in the region of undoubted muco-cartilage, a fatty degeneration of the cells frequently appears, together with an increase in the blood-spaces,—the precursor, in fact, of the great change which overtakes this tissue soon afterwards, at the time of transformation, when it is invaded by blood, and swept away, except in those places where new cartilage is formed. I conclude, then, that the tissue of this vascular space was originally muco-cartilage, which has degenerated during the life of the *Ammocoetes*. The fact that in most cases undoubted muco-cartilage

is to be found here and there in this space, is strong confirmation of the truth of this conclusion.

If this conclusion is a just one, we may expect that it would be confirmed by the embryological history of the tissue, and we ought to find that in much younger stages a homogeneous tissue of the same nature as muco-cartilage fills up the spaces in the branchial region, where in the *Ammocoetes* only blood and fat

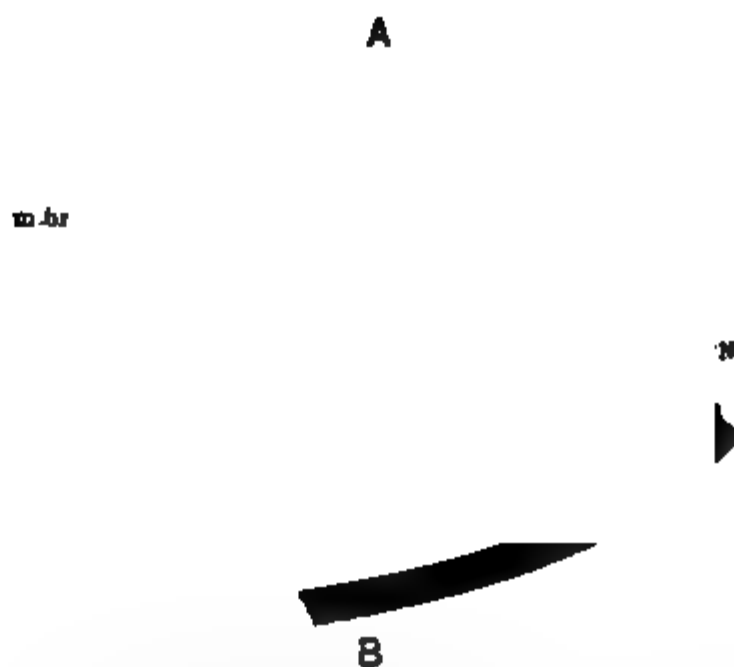


FIG. 25, A.—Muco-cartilage of lower lip (*Mc*); *m.pl.*, muscle of lower lip; *m.sm.*, somatic muscle; *Cor.*, laminated layer of skin.

B.—Degenerated muco-cartilage of branchial region. *F*, fat layer; *P*, pigment; *Bl*, blood space; *N*, somatic nerve; *m.br.*, branchial muscle; *m.sm.*, somatic muscle.

containing cells are present. For this purpose Shipley kindly allowed me to examine his series of sections through the embryo at various ages. These specimens are very instructive, especially those stained by osmic acid, which preserves the natural thickness of this space better than other staining methods. At an



age when the branchial cartilages are seen to be formed; when no fat cells are present, a distinctive tissue (fig. 26, B) is plainly visible in the velum and at the base of the tentacles, in the very position where in the more advanced *Ammocoetes* muco-cartilage exists. Taking, then, this tissue as our guide, the specimens show that the space between the skin and the visceral muscles in which the cartilaginous basket-work lies is filled with a similar material. At this stage a sheet of embryonic tissue occupies the position where, later on, blood spaces and fat cells

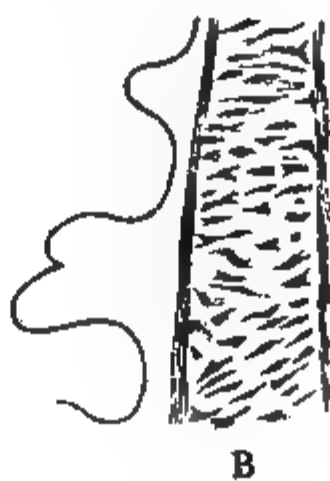


FIG. 26, A.—Muco-cartilage of velum.

B.—Embryonic muco-cartilage of tentacular bar.

are found, and this tissue resembles that seen in the velum and other places where muco-cartilage is afterwards found.

I conclude, therefore, that originally the branchial or mesosomatic region was covered with a dorsal plate of muco-cartilage, which carried on its under surface the dorsal part of the branchial basket-work, and sprang from the central core of skeletogenous tissue around the notochord; this plate was separated from the plate which covered this region ventrally by the lateral groove in which the gill-slits are situated. The ventral plate carried on its under surface the ventral part of the branchial basket-work, and was originally continuous with the plate over the thyroid gland.

In the figures on Pl. LVII. the head skeleton of *Ammocoetes* is represented from the dorsal, ventral, and lateral aspects. The muco-cartilage is coloured red, the branchial or soft cartilage blue, and the hard cartilage purple. The degenerated muco-cartilage of the branchial region is represented as an uncoloured plate,

on which the branchial basket-work stands in relief. If it were restored to its original condition of muco-cartilage, it would represent a uniform plate, on the *under* surface of which the basket-work would be situated; and if it were calcified and made solid, the branchial basket-work would not show at all in these figures.

Is it possible to find the reason why this skeletal covering has degenerated so early before transformation, and why the thyroid plate is left good until transformation? We see that all that part which has degenerated is covered over by the somatic muscles,—by, in fact, muscles which, being innervated by the foremost spinal nerves, belong naturally to the region immediately following the branchial. I suggest, therefore, that the original skeletal covering of muco-cartilage has remained intact only where it has not been invaded and covered over by somatic muscles, but has been invaded by blood and undergone the same kind of degenerative change as overtakes the great mass of this tissue at transformation wherever the somatic muscles have overgrown it.

The covering somatic muscles in the branchial region form a dorsal and ventral group, of which the latter is formed in the embryo much later than the former, the line of separation between the two groups being the lateral groove, with its row of branchial openings. This groove ends at the first branchial opening, but the ventral and dorsal somatic muscles continue further. It is instructive to see that, although the lateral groove terminates, the separation between the two groups of muscles is still marked out by a ridge of muco-cartilage (represented in fig. A, Pl. LVII.) which terminates anteriorly in the opercular bar.

Passing now to the prosomatic region, we find that here, too, the muco-cartilaginous external covering is divisible into a dorsal and a ventral head plate, the ventral head plate being the plate of the lower lip, and the dorsal head plate the plate of muco-cartilage over the front part of the head.

The staining reaction with thionin maps out this dorsal head plate in a most beautiful manner, and shows that the whole of the upper lip region in front of the nasal orifice is one large plate of muco-cartilage, obscured largely by the invasion of the crossing muscles of the upper lip, but left pure and uninvaded all

around the nasal orifice, and where the upper and lower lips come together. In addition to this foremost plate, a median tongue of muco-cartilage covers over the pineal eye and fills up the median depression between the two median dorsal somatic muscles. Also, two lateral cornua pass caudalwards from the main frontal mass of muco-cartilage over the lateral eyes, forming the well known wedge which separates the dorsal and lateral portions (*md*, *ml*, fig. 3, Pl. LVI.) of the dorso-lateral somatic muscle.

In fact, similarly to what we find in the branchial region, the muco-cartilaginous covering can be traced with greater or less completeness only in those parts which are not covered by somatic muscles. In the intact *Ammocoetes*, as seen in fig 3, Pl. LVI., representing the dorsal region of the front part of the head, the dorsal muco-cartilaginous plate, with its two cornua extending over the lateral eyes, and its median tongue covering over the brain and pineal eyes, is distinctly visible by its translucent appearance, in contradistinction to the opacity of the parts covered over by the somatic muscles.

In the figures on Pl. LVII. this striking muco-cartilaginous head shield, both dorsal and ventral, is shown. Seeing that the upper lip wraps round the lower one on each side, and that this most ventral edge of the upper lip contains muco-cartilage, as is seen in fig. 2, Pl. LVI., strictly speaking the dorsal head shield of muco-cartilage ought to extend more ventrally in the drawings. I have cut it short in order not to interfere with the representation of the lower lip and tentacular muco-cartilages.

From what has been said, it follows that the past history of the skeletal covering of the whole head region of *Ammocoetes*, both frontal and occipital, can be conjectured by means of the ontogenetic history of the foremost myomeres.

Dohrn<sup>1</sup> and all other observers are agreed that during the development of the animal a striking forward growth of the foremost somatic myomeres takes place, so that, as Dohrn puts it, the body musculature has extended forwards over the gill region, and at the same time the gill region has extended backwards. It is therefore probable that in the ancestral form the myotomes, innervated by the first spinal nerves, immediately succeeded the branchial region. Judging from *Ammocoetes*, the

<sup>1</sup> See Fürbringer, *op. cit.*, p. 592.

forward growth was at first confined to the dorsal region, invaded therefore the dorsal head plate, the ventral musculature being distinctly a later growth. With respect to this dorsal part of the myotomes, the first myotome is originally situated some distance behind the auditory capsule, and then grows forward towards the nasal opening; the lateral part, according to Hatschek, grows forward more quickly than the dorsal part, and splits itself above and below the eye into a dorsal-lateral part (*m d*, fig 3, Pl. LVI.), which extends up to the olfactory capsule, and a ventro-lateral part (*m l*, fig. 3, Pl. LVI.) (*m. lateralis capitis anterior superior*, and *inferior*), thus giving rise to the characteristic appearance of the muco-cartilaginous head shield of *Ammocoetes*.

If, then, the somatic longitudinal muscles supplied by the uppermost spinal nerves originally were situated immediately posterior to the region of the vagus nerves, the *Ammocoetean* animal would possess an external dorsal plate of muco-cartilage covering over the whole of the branchial and trigeminal region, and a ventral plate covering the branchial and thyroid region and the lower lip. These two plates would be separated from each other by the lateral groove in which the gill openings are found. The dorsal aspect of the head shield of such an animal would be fairly represented by fig. 10. If, further, the mucoid colloidal substance which forms the ground substance of muco-cartilage became calcified, then this modification of *Ammocoetes* would be enclosed in a hard dorsal and ventral head shield, resembling closely that of *Tremataspis* or *Didymaspis*. Further, the whole animal would take the appearance represented by fig. 27, which is a slight modification of Rohon's figure of a restored



FIG. 27.—Restoration of *Tremataspis* (after Rohon, slightly modified).

*Tremataspis*, in which the spinal skeleton is formed by the calcification of the massive connective tissue between the myotomes—the myo-commata—thus giving rise to an aponeurotic body skeleton exactly similar to that found in these old forms. In such an animal rapidity and freedom of movement would be

small if, as was the case in many forms (see fig. 29), the body region was short; and, as already stated, the embryological history of *Ammocetes* shows how greater mobility and freedom of movement was attained by the forward growth of the foremost myotomes over the cranial region between the outer skin

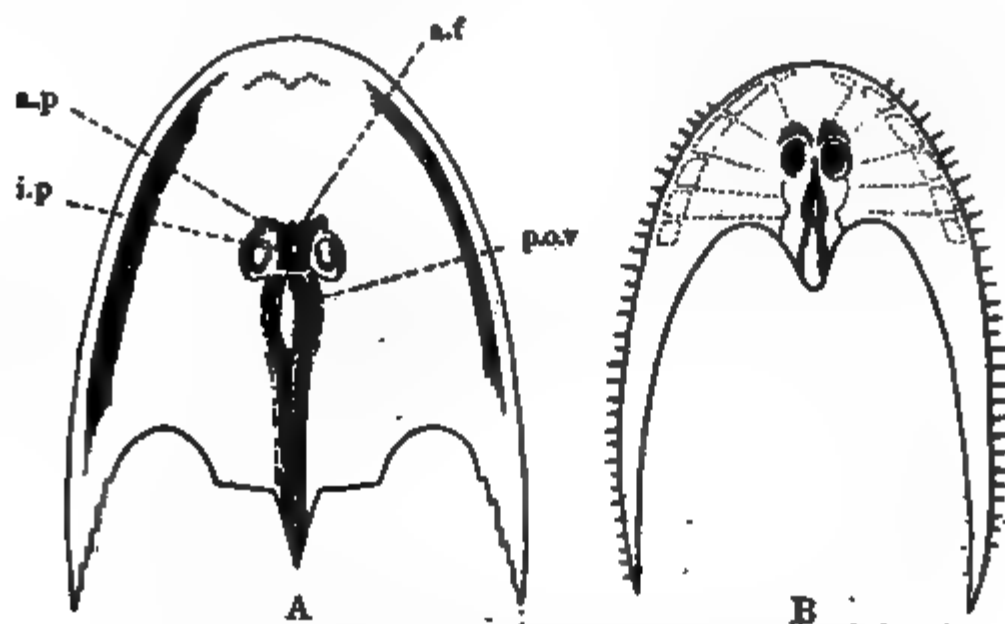


FIG. 28, A.—Dorsal head shield of *Cephalaspis* (from Lankester).  
B.—Dorsal head shield of *Keraspis* (from Lankester).

and the muco-cartilaginous skeleton. Such a growth would be a gradual one, and, judging from *Ammocetes*, would extend in the first instance laterally, and thus would give rise to a head shield of the type of *Auchenaspis* (*Thyestes*). The further growth of

FIG. 29.—*Auchenaspis* (*Thyestes*) *verrucosus*, natural size (from Woodward).

the foremost myotomes would reduce more and more the skeleton covering the branchial region, and more and more confine the head shield to the region of the trigeminal nerve, and we should get the various types of the *Cephalaspidæ* from *Cephalaspis* to *Eukeraspis*. Finally, in the fully developed *Ammocetes*, the

dorsal myotomes reach up to the nasal orifice, and the dorsal head shield of muco-cartilage has shrunk to the dimensions seen in *Ammocoetes*. Even then the same process continues, the somatic muscles extend still further forwards, when transformation takes place; but now, with the formation of the cartilaginous cranium efficiently protecting the brain region, all muco-cartilage disappears, and all that remains of the ventral and dorsal head plates of the *Cephalaspidæ* is to be found in some portions of the cartilaginous skeleton of the adult *Petromyzon*.

Such, then, is the significance of these muco-cartilaginous head plates which suggests itself by the study of *Ammocoetes* alone. The time has therefore come to consider the palæontological evidence, and to see whether it is in conformity with the conclusion deduced from the study of *Ammocoetes* alone.

The oldest known fishes belong to a large group of strange forms which inhabited the Silurian and Devonian seas, classed together by Smith Woodward under the name of Ostracodermi. These are divided into three orders:—1, the Heterostraci, including one family, the Pteraspidae, to which Pteraspis and Cyathaspis belong; 2, the Osteostraci, divisible into two families, the Cephalaspidæ and Tremataspidæ, which include Cephalaspis, Eukeraspis, Auchenaspis or Thyestes, and Tremataspis; and 3, the Antiarcha, with one family, the Astrolepidæ, including Astrolepis, Pterichthys, and Bothriolepis. Of these the first two orders belong to the Upper Silurian, while the third is Devonian.

Of these three orders the Heterostraci and Osteostraci are the oldest, and among them the Cephalaspidæ have afforded the most numerous and best worked-out specimens. At Rootziküll, in the island of Oesel, the form known as *Thyestes* (*Auchenaspis*) *verrucosus* is especially plentiful, being found thickly massed in among the masses of Eurypterid remains, which give the name to the deposit. Of late years this species has been especially worked at by Rohon, and many beautiful specimens figured by him, so that a considerable advance has been made in our knowledge of this form since Pander, Eichwald, Huxley, Lankester, and Schmidt studied these most interesting primitive forms.

All observers agree that the head region of these fishes was covered by a dorsal and ventral head shield, while the body

region was in most cases unknown, or, as in Eichwald's specimen, and in the specimens figured in Lankester and Smith Woodward's memoirs, was made up of segments which were not vertebral in character, but formed an aponeurotic skeleton, being the hardened aponeuroses between the body muscles. This body skeleton, which possesses its exact counterpart in *Ammocoetes*, will be considered more fully when I discuss the origin of the spinal region of the vertebrate.

Of the two head shields, ventral and dorsal, the latter is best known and characterises the group. It consists of a dorsal plate, with characteristic horns, which in *Thyestes verrucosus* (fig. 9), as described by Rohon, is composed of two parts, a frontal part and an occipital part (*occ.*), the occipital part being composed of segments, and possessing a median ridge, the *crista occipitalis*. In Lankester's memoir and in Smith Woodward's catalogue, a large number of known forms are described and delineated, and we may perhaps say that in some of the forms, such as *Eukeraspis pustuliferus* (fig. 28, B), the frontal part of the shield only is capable of preservation as a fossil, while in *Cephalaspis* (fig. 28, A) not only the frontal part but a portion of the occipital region is preserved, the latter being small in extent when compared with the occipital region of *Auchenaspis* (*Thyestes*). Finally, in *Tremataspis* and *Didymaspis* the whole of both frontal and occipital region is capable of preservation, the line of demarcation between these two regions being well marked in the latter species. The specimens of *Cephalaspis* in the British Museum,<sup>1</sup> in which the body skeleton and head shield are preserved in continuity, show how the former merges into the latter, and give strongly the impression of an invasion of the occipital part of the head shield by the aponeurotic spinal skeleton; an invasion, *i.e.*, as already suggested, of the head plate over the branchial region by the intrusive foremost spinal myomeres.

Lankester, in his monograph of the *Cephalaspidæ*, gives<sup>2</sup> the following restored outline sketch (fig. 28, A) of the head shield of *Eucephalaspis Agassizii* as typical of the group, with the following description:—"Between the orbits is a well-marked tubercle, which I call the *interorbital prominence (i.p.)*. In front of each

<sup>1</sup> Smith Woodward, Catalogue of Fossil Fishes, Part II., Pl. X., fig. 1.

<sup>2</sup> *Op. cit.*, p. 37.

orbit the material of the test is also raised into a projecting mass, which is to be called the *antorbital prominence* (*a. p.*). Between the two *antorbital prominences* is a very deep depression of the shield, divided beneath the superficial lamina into two parts by a narrow septum continued from the *interorbital prominence*, which is hollow. The two cavities thus formed are the *antorbital fossæ* (*a. f.*).” This very deep depression Lankester considers to be the olfactory cavity, and he lays special stress on its double appearance, and indeed says<sup>1</sup> that the Cephalaspidian fishes “disclose, upon careful examination, points of structure, such as the double olfactory cavities and the pectoral appendages, which place them very far above some living Vertebrata (Lampreys) classed as fishes.” Smith Woodward,<sup>2</sup> speaking of *Antiarcha* and the *Osteostraci*, does not recognise any narial openings in either case. He says:—“In the absence of narial openings in the cranial shield, both types also agree, and the olfactory organ, if present, must thus have retained its embryonic situation on the ventral aspect immediately in front of the mouth.” In this respect he does not accept Lankester’s evidence of the high position of these fishes; and with respect to Lankester’s proof of the pectoral appendages in *Cephalaspis*, he says they are not fins at all, but “it now appears, however, that the structures are merely a portion of the shield itself, divested of the outer and inner layers to ensure flexibility.”

The frontal part of the dorsal head plate carried, according to Rohon (fig. 9), the two orbits for the lateral eyes (*l.e.*), a marked frontal organ (*fro.*), and a median depression (*gl.*), to which he gives the name parietal organ. The occipital part (*occ.*) was clearly segmented, and carried, he thinks, the branchiæ. A similar organ to the frontal organ of *Thyestes* was described by Schmidt in *Tremataspis*, and considered by him to be a median nose. I reproduce Rohon’s figure of its appearance in *Thyestes* (fig. 30); he describes it as a deeply sunk pit, divided in the middle by a slit, which leads deeper in, he supposes towards the central nervous system. This median frontal nose and the two lateral eyes near the middle line are the well-marked characteristic of the whole of this group of fishes.

Clearly enough, Rohon’s frontal organ is the same as Lan-

<sup>1</sup> *Op. cit.*, p. 61.

<sup>2</sup> *Op. cit.*, Introduction, p. xix.



kester's double olfactory cavities; and the apparent discrepancy in the description of the two observers is cleared up immediately by comparing the two drawings with the corresponding structure in *Ammocoetes*. As we see, fig. 3, Pl. LVI., representing a surface view of the nasal orifice, is almost identical with Rohon's figure. If, now, the somatic muscles be removed, and the superficial parts of the nasal orifice and the neighbouring cranial walls be removed, the appearance thus produced is given in fig. 31, in which the nasal orifice now appears to be double, being divided partly by a septum, the whole appearance resembling most closely Lankester's picture. This appearance of a septum is due partly to the configuration of the nasal tube, bending as it does abruptly backwards, partly to the resistant character of the conjoined

FIG. 30.—Narial opening and lateral orbits of *Thyestes verrucosus* (from Rohon).

issue of the cranial wall and nasal cartilage. It is suggestive that Lankester himself says that the narrow septum divides the deep depression into two parts *beneath the superficial lamina*, as though the superficial parts had to be removed in order to obtain this appearance.

Such a description is absolutely compatible with the actual condition in *Ammocoetes*, and we see how closely his description agrees with the actual arrangement of parts of *Ammocoetes*. His antorbital prominence (*a.p.*) is the semi-annular termination of the nasal cartilage (see fig. 4, Pl. LVI., and C, Pl. LVII.), which would stand out if the soft parts were removed; his antorbital fossæ (*a.f.*) are the nasal tube, and his inter-orbital prominence (*i.p.*) is the pineal eye (*c.e.*).

When Rohon speaks of the post-orbital median depression as the parietal organ, he clearly does not really mean that this space

was all taken up by the median eyes; it is rather that the median eyes were in this space. The space itself clearly enough represents the position of the fore part of the cranium, as will be demonstrated later on.

Rohon's specimens and those described by Lankester and Smith Woodward all receive a complete explanation from the study of *Ammocoetes*, for we see that these fossil head shields are neither more nor less than the muco-cartilaginous head shield of *Ammocoetes*, as already indicated. If we restored the muco-cartilage of the branchial region, we should have, in the first place, Tre-

le

FIG. 31.—Head of *Ammocoetes*; most dorsal layers removed to show the appearance of the olfactory tube *na* and its position with respect to the cranial walls, the median eyes *ce*, and the lateral eyes *le*.

mataspis or *Didymaspis*, followed by *Auchenaspis*; if we leave it as it is, we have *Eukeraspis*. The intermediate stages shown in the *Cephalaspidæ*, between the extreme forms of *Auchenaspis* and *Eukeraspis*, are simple indications of the extent of the forward growth of the somatic muscle, with the corresponding increase of mobility in the fish. The *Ammocoetes* shows how the immobile armour plate of the original *Eurypterid*-like fish succumbed to the forward growth over it of the spinal musculature, and so

led to the freer and more mobile form of the rapidly moving *Ammocoetes*.

The ventral head plate was clearly the ventral muco-cartilaginous plate of *Ammocoetes*; there were no jaws, no teeth, but in all probability a flexible upper and lower lip of the *Ammocoetean* type. The final evidence that such was the case, and that the *Ammocoetes* is in reality a slightly modified *Cephalaspid*, is seen in the identity of structure between the muco-cartilage and these fossil so-called bony shields.

I will not attempt here to discuss in detail the nature of the structure of the head shields of the *Pteraspids* and of the *Cephalaspids*; it is sufficient to state that the former are characterised by the regularity of the lamination of their layers, in which no sign of bone cells are found, while the latter are composed of the so-called bone structure.

The whole question of the meaning of the structure of the skin of *Ammocoetes*, with its wonderfully regular laminated layer underlying the epithelium, will form a separate part of this series of papers, and will, I, hope, follow immediately upon the next parts dealing with the auditory and optic nerves; here I simply want to consider the muco-cartilaginous skeleton of the head, and its relation to the so-called bony plates of the *Cephalaspids*.

Rohon's picture, which I here reproduce (fig. 7, Pl. LVI.), is the latest and best figure of the structure of this so-called bone. It is, as he describes, clearly composed of fibrillæ and star-shaped cells, arranged more or less in regular layers, with other sets of similar cells and fibrillæ arranged at right angles to the first set, or at varying angles. The groundwork of this tissue, in which these cells and fibrils are embedded, contained calcium salts, and so the whole tissue was preserved. In places, spaces are found in it, in the deepest layer large medullary spaces, more superficially ramifying spaces, which he considers to be blood-vessels, and calls Haversian canals; the star-like cells, however, are not arranged concentrically around these spaces, as in true Haversian canals.

If we turn now to the structure of muco-cartilage, we see how remarkably similar it is; we see the same star-like cells and fibrillæ arranged more or less in layers as Schaffer has

described; arranged, as a rule, at right angles to the bounding layers of perichondrium, as Schneider has described (*cf.* fig. 25, A).<sup>1</sup> Schaffer says expressly that in the plates of muco-cartilage of the upper lip they are not arranged so regularly at right angles to the perichondrial layers as in the plate of the lower lip or the thyroid plate, but take various directions.<sup>2</sup> He also states that the shape of the cells is such that they appear broad and star-like in sections parallel to the surface, and spindle or rod-like in sections at right angles, so that in any section this difference of appearance enables us to draw conclusions as to the arrangement of the plates. In fig. 6, Pl. LVI., I give a specimen of muco-cartilage in the head region, taken from a series of horizontal sections stained with osmic acid. It is seen that the cells and fibrils are arranged partly at right angles to the limiting layers, partly in the direction of these layers; and on the whole, the cells in the one direction are broader and more star-shaped, and in the other more spindle or rod-shaped, as described by Schaffer.

The whole structure is clearly remarkably like Rohon's picture of a section of the head plate of a Cephalaspid. In the latter case the groundwork contains calcium salts, in the former it is the peculiar homogeneous mucoid tissue which stains so characteristically with thionin. With respect to this calcification, it is instructive to recall the calcification in the interior of the branchial cartilages of *Limulus*, as described in Part II. of this series of papers, as showing how easy it is to obtain a calcification in this chondro-mucoid material. With respect to the medullary spaces and smaller spaces in this tissue, as described by Rohon, I would venture to suggest that they were not necessarily all blood-vessels, for similar spaces would appear in the head shield of *Ammocoetes* if its muco-cartilage alone were preserved. Of these, some would be blood-vessels, such, for instance, as the external carotid which traverses this structure; but the largest and most internal, forming spaces like Rohon's medullary spaces, would be muscular, being filled up with bundles of the upper lip muscles.

Seeing the unique character of this muco-cartilaginous skeleton in *Ammocoetes*, seeing the importance of muco-cartilage as the

<sup>1</sup> *Op. cit.*, p. 638.

<sup>2</sup> *Op. cit.*, p. 641.

forerunner of cartilage (Vorknorpel), it is only what one would expect to find that the earliest vertebrate skeleton was a calcified muco-cartilage. So, also, in accordance with my interpretation of the meaning of the transformation, the total disappearance of this tissue at transformation is only what one would expect.

*The Larval Cephalaspid a Eurypterid.*

From what has been said, we may consider that Ammocoetes demonstrates to us the nature of the Cephalaspids; in other words, the adult condition of these ancient fishes resembled the larval condition of the Petromyzon. As a necessary corollary to this conclusion, the developmental history of Ammocoetes may fairly be taken to represent, in an abbreviated form, the early stages of the Cephalaspids, so that if there is evidence of a larval condition in Ammocoetes, we may be sure that the Cephalaspid possessed a larval stage, the nature of which is indicated by this early condition of Ammocoetes. It is, therefore, a matter of exceeding interest, as throwing a strong light on the origin of the Cephalaspids, to find that Kupffer<sup>1</sup> lays great stress on the existence of a larval stage in Ammocoetes itself. This stage exists, according to him, up to the length of 5 mm., and then with considerable suddenness a transformation occurs which results in the production of the Ammocoetes itself. During this larval stage the oral chamber is still closed, the opening of the tube of the hypophysis, *i.e.*, the olfactory tube, is ventral, so that the dorsal head shield, if it were represented at this stage, would have the appearance seen in fig. 8, B, and not that in fig. 8, C, *i.e.*, would represent in the arrangement of its parts a Eurypterid rather than a Cephalaspid. Between the 5 mm. and 6 mm. stage, the whole system of epibranchial ganglia in connection with the trigeminal vanishes with great rapidity (a disappearance, *i.e.*, of the separate ganglia connected with the endognaths and ectognath, indicating the dwindling and reduction of these appendages), the oral chamber communicates with the branchial chamber, and the

<sup>1</sup> *Op. cit.*, Heft. 3. "Die Entwickl. d. Kopfnerven v. Ammoc. Planeri. Dritter Abschnitt." *Die Metamorphose des larvalen Nervensystems des Kopfes*, p. 51, 1895.

nasal opening becomes dorsal by the forward growth of the upper lip.

These observations of Kupffer give the strongest possible hint that the Cephalaspid passed through a larval stage, which terminated with a transformation into the adult condition, just as the Petromyzon passes through a larval stage, ending with a transformation, or the Amphibian passes through the tadpole stage. Just as the larval stage of the Amphibian—the tadpole—is of the nature of Petromyzon, and the larval stage of Petromyzon is a Cephalaspid, so the larval stage of the Cephalaspid was Eurypterid in form, with the two lateral eyes and the median eyes in position, and the position of the primordial cranium marked out by the glabellum; at transformation with the breaking through of the oral chamber between the gnathobases of the metastoma, the closure of the larval mouth by the growth of the plastron or primordial cranium, and the forward growth of the endostoma to form the anterior part of the head shield, with the consequent formation of the dorsal nasal orifice, the larval Eurypterid would transform into the adult form, *i.e.*, the Cephalaspid or Ammonoites. Thus the prosomatic carapace of the Eurypterid becomes transformed into the frontal region of the Cephalaspid, and the mesosomatic carapace into the occipital region.

Step by step the consideration of the cranial nerves, of the central nervous system, of the muscular and skeletal systems in the cranial region, from an anatomical, an embryological, and a physiological point of view, has led us to the conclusion that the larval stage of the Cephalaspid was Eurypterid in nature, or at all events, something between a Trilobite and a Eurypterid. At that period of the earth's history, in the Silurian seas, when these earliest fishes first made their appearance, the masters of the deep were the giant Eurypterids; the dominant race were the Merostomata, which in their turn had developed from the preceding Trilobites, swarms of which still occupied the seas. Always, wherever the Cephalaspids are found, often imbedded in the same mass of stone, are found specimens of Eurypterus, of Bunodes, of Hemiaspis, or one or other of these Eurypterid forms. All the conditions were exactly favourable to the evolution of a higher type from the dominant race of this time, *i.e.*, from the Eurypterid type. Is there any strong drawback, any serious difficulty

in the way of such evolution? What view is taken by palæontologists as to the alliance of these primitive fishes with invertebrate forms?

Smith Woodward says<sup>1</sup>—"They pertain either to the class Pisces, or to some lower denomination yet to be determined. Though placed in immediate association with the Urochorda and Agnatha by Cope, and lately supposed to be allies of the Arachnids by Patten, few facts can be adduced in favour of either of these theoretical interpretations of the group. The Arachnid theory is based upon a complete misapprehension of the most fundamental points in Ostracoderm skeletal anatomy; while the comparison of the dorsal opening in the cranial shield of the Asterolepida with the mouth of an Ascidian, as originally made by Cope, is already admitted by that author himself to prove untenable."

When Smith Woodward thus contemptuously dismissed the Arachnid theory, it was a pity that he ignored all consideration of my theory of the origin of vertebrates, and therefore of these early debatable vertebrate forms, as though the Arachnid theory was solely represented by the impossible supposition of Patten that the dorsal (neural) head surface of fishes is comparable with the ventral(neural)prosomatic surface of the Merostomata. Seeing that my views of the origin of Vertebrates from the Merostomata had been before the world for two years before they were travestied by Patten, and seeing also, as is shown in his own catalogue, the frequency with which the head shields of the Osteostraci or portions of them have been originally described as portions of a Eurypterus, the Arachnid theory cannot be dismissed by simply pointing out the absurdity of Patten's views.

I would submit to the consideration of Smith Woodward and other palæontologists the question whether these forms are not exactly of the kind which might be expected to have existed if the earliest fish was intermediate between the Merostomata and Ammocetes. The whole appearance of them vividly recalls to mind the Trilobites, the Limuli, and the Merostomata, the frontal part of the shield forming the prosoma and the occipital part the mesosoma.

<sup>1</sup> *Op. cit.*, p. 17.

*The Primordial Cranium of Rohon.*

One difficulty remains which requires consideration. If these fishes were directly derived from Eurypterid-like forms, one ought reasonably to expect that the prosomatic appendages would be more conspicuous than in *Ammocoetes*, and that they ought to show in the fossils. On the other hand, such undoubted Eurypterids as *Hemiaspis*, *Bunodes*, etc., show no sign of free prosomatic appendages. Either their appendages were hidden between their dorsal prosomatic carapace and some ventral metastomal plate, or were perishable, and have not been fossilised.

As to the mesosomatic branchial appendages, they are naturally hidden away as the branchiæ in the occipital region of the Cephalaspids, as in the Merostomata; but some remnant of the prosomatic appendages ought to be found under or in connection with the frontal region. According to my arguments deduced from *Ammocoetes*, these prosomatic appendages were covered in ventrally by the metastoma, *i.e.*, the anterior part of the ventral head shield of the Osteostraci; any sign of them, therefore, must be looked for between the dorsal and ventral head shields; and if it be found that this portion of the animal was divided into well-marked segments, each of which might reasonably be the only indication of such a prosomatic segment and appendage, then it seems to me that the evidence of an origin from such scorpion-like forms becomes very strong.

Such evidence has been lately given by Rohon, who, in further investigations on *Thyestes verrucosus*, has made a most interesting discovery, which he terms the segmentation of the primordial cranium. He has discovered specimens in which the dorsal shield has been removed, and so we are able to see what that dorsal shield covered.

In fig. 32 I reproduce his drawing of one of his specimens from the dorsal and lateral aspects. These drawings show that the frontal part of the shield covered a markedly segmented part of the animal; he sees five distinct segments apart from the median most anterior region. This segmented region is entirely confined to the prosomatic region, *i.e.*, to the region innervated



by the trigeminal nerve. His drawing looks for all the world as though we were seeing here in this most primitive fish the last traces of the prosomatic appendages, and in any case lends most powerful support to the view put forward in this paper, that the trigeminal nerve originally supplied at least five segments. An indication of similar markings is given in Lankester's figure<sup>1</sup> of *Eukeraspis pustuliferus* (see fig. 28, B), and, indeed, evidence of a segmentation under the antero-lateral border of the head shield

FIG. 32.—Lateral and dorsal views of the frontal and occipital regions of the head shield of *Thyestes*, after removal of the outer surface (from Rohon).

is recognised at the present time, not only in the Cephalaspidæ, but also in the Pteraspidæ, as was pointed out to me by Smith Woodward in the specimens at the British Museum.

These specimens of Rohon are of very great importance for the estimation of the nature of these earliest fishes, and I will therefore state what, in my opinion, is the interpretation of this discovery of Rohon's. He calls these segments discovered by him the segmentation of the primordial cranium; it would, I think, be better to call it the segmentation of the anterior region of

<sup>1</sup> *Op. cit.*, p. 58.

the head, for that is really what his figures show, not necessarily the segmentation of the primordial cranium. Let us consider this matter in the light of my theory. As already mentioned, the prosomatic carapace of most if not all the forms like the Hemiaspidæ, etc. (see figs. 6 and 7), is marked out into segments in a manner strikingly resembling the segments discovered by Rohon: the meaning of this segmentation in the front part of the head of these extinct forms which were intermediate between the phyllopod trilobites and the living king crabs and scorpions can be deduced with the greatest probability, by seeing to what the similar segmentation on the carapace of such forms as *Mygale* and *Phrynus* is really due. As already mentioned, these markings on the carapace are formed in the latter cases by the attachment of the prosomatic appendages to the carapace, as is seen in fig. 5, which represents the arrangement of parts seen in *Phrynus* on removal of the carapace, the limit of the carapace being indicated by the outside line.

In such forms as is seen by the comparison of fig. 4 with fig. 5, the markings on the exterior indicate quite clearly the limits of the important structures beneath. Only the central unsegmented portion (*glab.*) covers over that part which is occupied by the brain and alimentary canal; this portion clearly corresponds to what is called by Woodward the glabellum in the Hemiaspidæ, etc. (*gl.*, fig. 7), the name being given in accordance with the similar name used in the description of the Trilobites. I shall therefore use the term 'glabellum' to indicate this central unsegmented plate, which covers over the brain region in all cases, whether classed among the fishes or the invertebrates, where such a structure is found. The limits of the space covered over by the glabellum is marked out in *Phrynus*, as already discussed in Part VI., by the upturned walls of the plastron or ento-chondrite, which form a primordial cranium, just as the thickened lateral bars of the same plastron formed the primordial trabeculæ (see Part II.).

I conclude, therefore, that the part of the carapace which corresponds to the cranium in the vertebrate is that central part called the glabellum, to the right and left of which the lateral orbits were situated.

If we now turn to the Cephalaspid head shield, we find here

also a central plate which, so Smith Woodward informs me, existed both in the Cephalaspidae and the Pteraspidae, and was of a different consistency to the rest of the shield, being harder for the protection of the vital brain region below it. This central plate or glabellum corresponds in position to Rohon's parietal organ (fig. 9, *gl.*), and to the post-orbital depression of Lankester (*p.o.v.*, fig. 28, A). Rohon, in his most recent paper,<sup>1</sup> referring to the specimens just mentioned, which show the lateral segmentation, describes this median structure as a "stabförmiges oder strangförmiges Gebilde," which arises in the middle of the posterior wall of the frontal organ, and after a short course, melts into the hinder or occipital part of the cranium. He speaks of it as a Leiste (ledge), and says that the two orbits are situated on the right and left side of this ledge.

The comparison of A, fig. 33, which represents the carapace of *Thyestes* with Rohon's segments marked on it, and of B, fig. 33, which represents the carapace of *Bunodes*, with lateral orbits

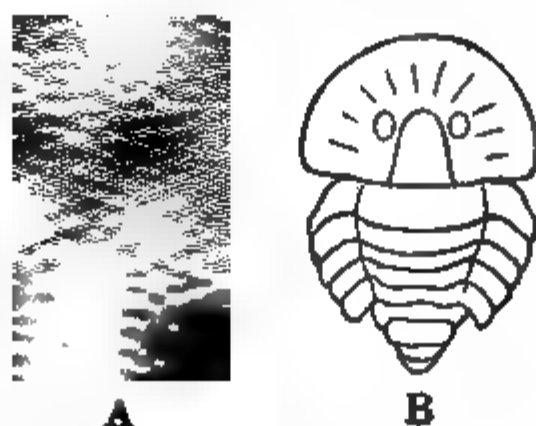


FIG. 33, A.—Outline of *Thyestes verrucosus* with Rohon's segments indicated.

B.—Outline of *Bunodes luvula* with lateral eyes inserted. Both figures natural size.

inserted so as to represent an old generalised semi-trilobite semi-scorpion form, shows how the two forms may be compared, the main difference between the two figures being the inclusion into the head shield of the fish of the olfactory opening, a consequence, as already explained, of the formation of the new *Ammocætean* mouth. Such comparison suggests most strongly that the limits of the cranium in *Thyestes* were marked out by

<sup>1</sup> "Weitere Mittheilungen über die Gattung *Thyestes*," *Bull. de l'Acad. de St. Pétersb.*, 5th series, vol. iv., 1896, p. 238.

the plate of the glabellum, just as the limits of the primordial cranium were marked out by the glabellum in the invertebrate.

Such a conclusion is made a certainty by comparing the head shield of *Thyestes* with the head region of *Ammocoetes* (fig. c, Pl. LVII.). Here also is a median structure (*cr.*) of elongated shape, which arises from the middle of the posterior wall of the nasal organ, and extends into the occipital part of the head. On the right and left side of this median structure the two orbits (*le*) are situated. Clearly this structure, which is the membranous cranium of the *Ammocoetes*, corresponds absolutely in position with this median *Leiste* (ledge) described by Rohon.

The very presence of this hard median plate or glabellum as a protection to the vital brain region makes it probable that the Cephalaspid cranium was membranous like that of *Ammocoetes*, or even was still only half formed from the plastron, as in *Galeodes* or *Phrynus*.

In conclusion, the evidence of comparative anatomy is very strong that Rohon's observation does not indicate the segmentation of the primordial cranium, but rather shows that these most primitive fishes possessed on each side of their cranium, in the region supplied by the trigeminal nerve, five well-defined segments, due, in all probability, to the presence of five pairs of prosomatic appendages. Such appendages were concealed ventrally by the lower head shield or metastoma; they were, in all probability, of the same nature as the appendages in *Bunodes* and *Hemiaspis*; and judging from Beecher's investigations on the Trilobite appendages, were quite possibly chiefly composed of gnathobases, their palps being reduced to tentacles after the fashion of *Ammocoetes*.

So, also, we see written plainly in the records of the lamprey why the cartilaginous and bony cranium of the vertebrate arose; how the protection of the external carapace gave place to the protection of the internal cranium. First, the chitinous carapace of the Eurypterid formed an efficient protection for the vital organs beneath. Then, when the Eurypterid became transformed into the Cephalaspid, the chitinous carapace was replaced by the calcified head shield of the Cephalaspids, and still the vital nervous organs were protected by an external shield. Then, for the sake of greater mobility and flexibility, the Cephal-

aspid somatic muscles passed further and further headwards, and the head shield of the Cephalaspid dwindled to the muco-cartilaginous external skeleton of the Ammocetes, which, still in its calcified form, protected the brain, until, with the conversion of the fibrous into the cartilaginous cranium, and the disappearance of the muco-cartilage, as seen at transformation, the last remnant of the Cephalaspid external skeleton vanishes, and henceforth the protection of the brain region is undertaken by the internal cartilaginous and bony cranium—the original internal primordial cranium of the Eurypterid.

Such, then, in my opinion, is clearly the nature of the Cephalaspidian head shield. It has been suggested that these segments along the antero-lateral border of the shield were branchial, and that the long cornua acted as opercula over the branchial openings. It seems to me very evident that the segments are too far forward for the ordinary branchial segments (and that is the proposition that these are branchial segments belonging to the vagus group of nerves), and that the comparison of this region with that of Ammocetes makes it most probable that this region was innervated by the trigeminal nerve, and therefore the branchial segments were situated, as Lankester, Schmidt, Rohon, etc., thought, in the occipital region. At the same time, it is perfectly possible, and indeed probable, that the reason for the extension of the calcified muco-cartilaginous head shield in the shape of the two cornua was because such cornua acted as opercula to the branchial openings, so that, as Smith Woodward suggests, Lankester's pectoral fin was of the nature of an operculum, for all such cornua would extend over the greater part of the branchial region, and cover it laterally and ventrally, if the occipital part of the head shield was branchial. In connection with this suggestion, it is to my mind significant that the trigeminal nerve in Ammocetes should supply a ventral strip of skin surface along and ventral to the line of branchial openings, which extends as far backwards as the 4th branchial segment (fig. 5, Pl. LVI.).

Further, it has been suggested<sup>1</sup> that these cornua may have formed part of the covering of an atrial cavity, and that something of the nature of an atriopore exists on each side in many

<sup>1</sup> G. B. Howes, *Nature*, vol. lxi. p. 309.

specimens, a suggestion which seems to me worthy of a deal of thought and careful consideration. I have always felt, as already mentioned, that the marked atrial cavity of *Amphioxus* must have originated from a primitive atrial cavity in an *Ammocoetean* fish, and must be explained in any exhaustive series of papers dealing with the origin of Vertebrates. So far, I have merely stated<sup>1</sup> that Fürbringer's suggestion appears to me most likely, and at present I will say no more. The discussion of this question cannot be undertaken until the position of the spinal nerves is made clear; I will therefore leave it until I have completed what I have to say on the cranial nerves, and then I hope to discuss the whole spinal region.

In conclusion, I will sum up the evidence of this Part. It is absolutely clear that *Ammocoetes* is a Cephalaspid; and judging from the evidence given in the development of *Ammocoetes* itself, a larval form of the Cephalaspid existed which was of the nature of a Eurypterid. Again, judging from the evidence given in the development of *Limulus*, the larval form of the Eurypterids was of the nature of a Trilobite, and the evidence of Beecher shows that the Trilobite was a Phyllopod, which was almost certainly derived from a Chætopod. On the other hand, the evidence given in the development of *Petromyzon* shows that the larval form of the *Petromyzon* was a Cephalaspid; while the *Petromyzon* itself, according to the researches of Parker and others, resembles the larval form of the Amphibian. From the Amphibian we pass to the Mammal, and from the Mammal to Man. Thus the study of *Ammocoetes* has enabled us to indicate the chain of evolution, owing to the enormous value of larval forms, from the Annelid to Man.

<sup>1</sup> Part III., *this Journal*, vol. xxxiii. p. 183.

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## DESCRIPTION OF FIGURES, PLS. LVI. AND LVII.

## REFERENCE LETTERS.

*br*<sub>1</sub>—*br*<sub>8</sub>, branchiæ; *sk*<sub>1</sub>—*sk*<sub>5</sub>, skeletal bars; *m*<sub>1</sub>—*m*<sub>5</sub>, striated visceral muscles; *mt*<sub>1</sub>—*mt*<sub>4</sub>, tubular muscles; *j.v.*, jugular vein; *m.v.*, maxillary vein; *na.*, nasal epithelium; *na. cart.*, nasal cartilage; *m. cart.*, muco-cartilage; *l.e.*, lateral eyes; *c.e.*, pineal eyes; *cr.*, cranium; *tr.*, trabeculæ; *ped.*, pedicle; *inf.*, infundibulum; *nc.*, notochord; *aud.*, auditory capsule.

## PL. LVI.

Fig. 1. Horizontal section of anterior part of *Ammocoetes* immediately ventral to the auditory capsule. V, trigeminal nerve.

Fig. 2. Sagittal lateral section through the head end of *Ammocoetes*.

Fig. 3. Dorsal view of intact head of *Ammocoetes*; *olf.*, olfactory organ; *md.*, *ml.*, dorsal and lateral parts of the foremost dorso-lateral somatic muscle.

Fig. 4. Horizontal section of anterior part of *Ammocoetes*, through pineal eye and nasal tube.

Fig. 5. Distribution of trigeminal nerve in *Ammocoetes*; *ps. br.*, pseudo-branchial groove; *met.*, nerve to lower lip, or metastomal nerve; *t.*, nerve to tongue; *tent.*, nerve to tentacles.

Fig. 6. Section of muco-cartilage from dorsal head-plate of *Ammocoetes*.

Fig. 7. Section of head-plate of *Cephalaspid* (from Rohon).

## PL. LVII.

Skeleton of head region of *Ammocoetes*—

A, lateral view.

B, ventral view.

C, dorsal view.

Muco-cartilage, red; soft cartilage, blue; hard cartilage, purple.





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PROCEEDINGS OF THE  
ANATOMICAL SOCIETY OF GREAT BRITAIN  
AND IRELAND.

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JULY 1899.

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A Summer Meeting of the Society was held in the Anatomical Schools, New Museum, Cambridge, on Saturday, 8th July, at 2.30 p.m. The President, Professor A. MACALISTER, F.R.S., was in the chair. Thirty-one members and eleven visitors were present. Letters regretting their inability to attend, were received from Professor Waldeyer, Professor Young, Professor Symington, Dr R. J. Berry, and Professor Birmingham.

The minutes of last meeting were read and confirmed.

Dr CHARLES J. PATTEN, B.A., Chief Demonstrator in Anatomy, Trinity College, Dublin, proposed by D. J. Cunningham, A. M. Paterson, and A. Keith, was elected a member of the Society.

(1) Professor SIDNEY MARTIN, F.R.S. (introduced by Professor Thane), showed *a Heart*, in which the left auricle was divided by a horizontal septum into a superior and inferior compartment. Similar specimens were shown by Dr Wardrop Griffith and Dr Rolleston at the meeting of the Society held on 10th February 1896.

(2) Dr WARDROP GRIFFITH showed *two examples of Moderator Band in the Left Ventricle* of the heart. In the first specimen the band arose by two fan-shaped processes from one of the columnæ carneæ, which was stretched out over the anterior part of the base of the anterior papillary group of muscles. These soon joined, and the resulting band, which was about half a millimetre in thickness, passed across the ventricle, and was inserted into the septum by an expanded base, about  $\frac{3}{4}$  inch below the junction of the anterior and postero-right aortic segments. Its total length was 2 inches, and it was devoid of muscle except where the muscle of the ventricle was drawn out into it at its attachments. The second specimen which is shown in the

*f*

outline diagram (fig. 1) strongly resembled the first, differing from it only in minor particulars. In commenting on these specimens Dr Griffith referred to the two examples described by Sir William Turner, who was, he thought, the first to call attention to the subject.

In Turner's first communication (*Journal of Anat. and Phys.*, vol. xxvii. p. xix) three bands were mentioned passing from the septum to the posterior wall, and one band 26 mm.  $\times$   $\frac{3}{4}$  mm., passing from the "base of the anterior papillary muscle to the septal wall." In his second

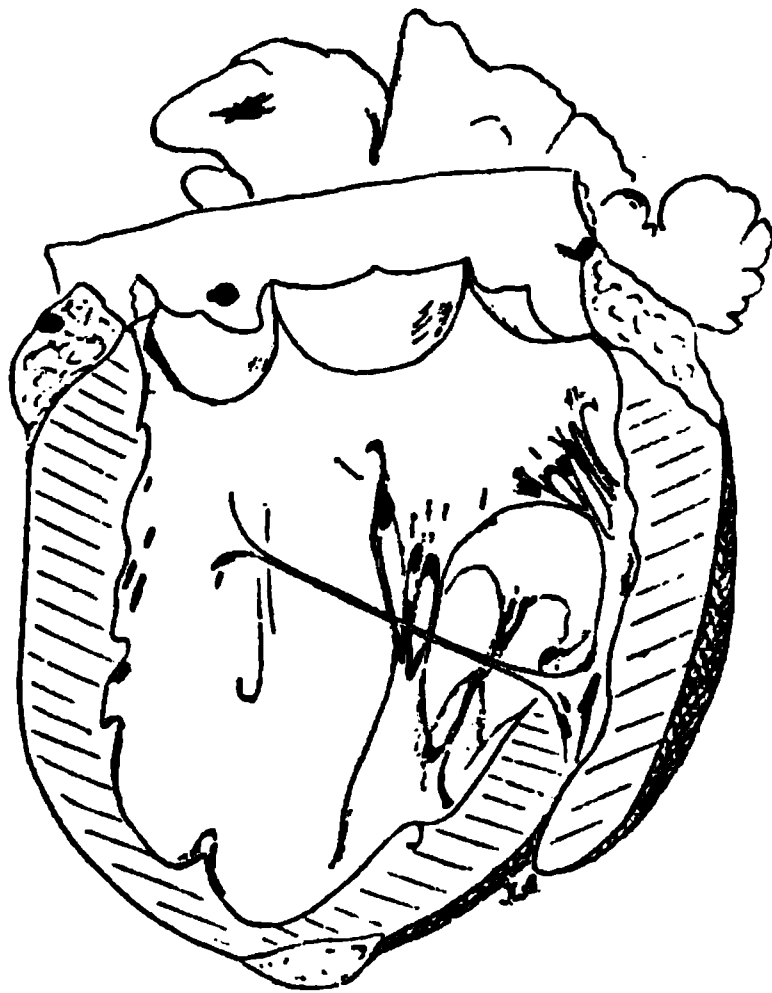


FIG. 1.—Moderator Band.

communication (*ibid.*, vol. xxx. p. 568), a band was described passing from the septum to an attachment "in intimate relation with the origin of the large papillary muscle."

Turner expressed the view that these bands are often present, but get cut in opening the heart. Dr Griffith thought that this was true as regards the smaller bands, and he had found many examples of such, showing a gradual transition to columnæ carneæ of the second variety, between which and these bands it was impossible to draw the line; but he thought the bands passing from the root of the anterior papillary muscle to the septum, mentioned by Turner in his first and second communication, and of which two additional examples were now shown, were somewhat rarer. The great similarity of the bands and of their attachment in these four specimens was suggestive of their having some morphological importance. The general deficiency of columnæ carneæ noted by Turner was not, Dr Griffith thought, a feature of the specimens now shown.

Dr WARDROP GRIFFITH also showed a *Heart* (fig. 2) with a band pass-

ing from the posterior group of papillary muscles up through the mitral orifice to the margin of the valve of the foramen ovale. At its papillary attachment it differed in no respect from one of the adjacent cordæ tendinæ, while further up it thickened irregularly, and was rigid and clearly calcareous in its core at its upper end. The heart was from a young subject, and there were no calcareous changes elsewhere in the organ. There were no cardiac symptoms, nor is it believed cardiac signs during life, and the action of the mitral valve

FIG. 2.

would doubtless be perfect. Dr Griffith believed the condition had not been previously described.

Dr WARDROP GRIFFITH also showed dissections of *three specimens of Imperforate Anus*. Two were examples of the form known as atresia ani urethralis. In the third example the condition was associated with so-called hermaphroditism, and the specimen will be described in full hereafter.

(3) Professor JAMES MUSGROVE exhibited *Specimens of Negro Skin* from the palm and anterior aspect of the trunk, prepared so as to show the various strata.

(4) Professor A. C. HADDON, F.R.S., exhibited and made remarks on *Specimens of Anthropological Interest obtained in New Guinea and Borneo*, during his recent expedition. The time had been too short since his return to allow him making an exhaustive investigation of the collection of skulls brought home, but the specimens obtained from the interior of Borneo, probably the largest number obtained up

to the present time, did not appear to indicate the presence of a negroid people in the Bornean Hinterlands.

(5) Dr R. J. BERRY exhibited stereoscopic photographs of the *Saphenous Opening* and *Anticubital Fossa*, to show their utility for teaching purposes.

(6) The next communication was made in the Museum by Mr W. L. H. DUCKWORTH—“*Notes on the Anthropological Collection in the Museum of Human Anatomy, Cambridge.*”

The Anthropological Collection occupies ten cases in the Museum of Human Anatomy, wall-cases being arranged round the sides of that room, in addition to five spacious central cases. The contents of these cases represent the results of the efforts of Professor Macalister and his predecessor in the Chair of Human Anatomy, the late Sir George M. Humphry, to bring together a thoroughly representative series of the crania of the various human races. With such success have those efforts been met that the Collection is second to none in this country, and comprises more than one subsidiary collection—*ex. gr.*, the Thurnam and the Hutchinson collections, of very considerable magnitude.

The very number of the specimens, however, renders the acquisition of a comprehensive knowledge of the contents of this Museum a matter of prolonged study, and it is with the idea of pointing out the rarer and more interesting examples that these notes have been brought together. At the same time, references are given to various periodicals in which certain portions of the Collection may be found described in detail.

It is convenient to describe the specimens in the order of the cases in which they are contained, and a rough sketch-plan of the Museum is appended in which the cases are marked with numerals from 1–10.

Thus, on entering the Museum, there will be found immediately to the left, a wall-case (No. 1) containing (besides some bones of the skeleton possessing no special anthropological importance) a series of modern European crania, of which the following are the most interesting:—

(a) Two skulls of Finlanders presented by Professor Retzius. The interest of these specimens lies in the fact that there has been a difficulty in determining the precise relationship of the Finns to other European nations, some Mongolian affinities having been suspected.

(b) The skulls of Lapps are also of interest in consideration of the obscure relationships of that race; and the similarity of these skulls to certain crania of Savoyard origin is marked.

(c) A cast of the cranium of King Robert Bruce will be found here; and that the statement repeated by various authors as to the Neanderthaloid characters presented by it, rest on a slender basis, will be seen on reference to the next case, No. 2, which stands beyond the wall-case containing the preceding specimens, and contains



plaster models of the crania of some of the classical examples of pre-historic man; among which will be found the following, referable to Palæolithic Man—viz.: the Neanderthal, Spy, and Engis crania;

(a) Aboriginal Australian (2115).      (b) Aboriginal Tasmanian (2096).

FIG. 1.

and of those of later date: the Cro-Magnon skull (early Neolithic period). Furthermore there is a cast of the Calvaria found by Dr Dubois in the Pliocene strata of Trinil, Java; it is attributed by its

(a) Female (3342).

b) Male (3324).

FIG. 2. —Natives of New Britain (Willey Coll.).

discoverer to a form known as *Pithecanthropus erectus*, which is justifiably supposed to represent a precursor of Man. A cast (2101) shows the cranium of an Australian aboriginal with some very pithecoïd features.

Turning back from case No. 2 towards the door, there will be found a case (No. 3) containing a variety of skulls, of which the following are on that aspect of this case facing the door:—

(a) The crania of aborigines of Tasmania (a race now extinct; *cf.* Nos. 2096–2100); and in close proximity to these,

(b) The crania of Australian aborigines—Nos. 2101–214 (for crania of Tasmania and Australian aborigines, see fig. 1); with the latter are three specially prepared heads of Australian natives, showing the wavy (not woolly) nature of the hair, and the plentiful beard; No. 2115 (*cf.* fig. 1) shows an extreme degree of prognathism, a character very constant in aboriginal Australians (ref. No. 1).

(c) Melanesian crania, especially the “Willey Collection” (brought to Cambridge by A. Willey, Esq., M.A., late Balfour-student), from the Melanesian island of New Britain, occupy much of the remaining space on this aspect of case No. 3. The following are points of interest in connection with this (otherwise) very homogeneous group: (i.) the great difference sometimes met with in the crania of the two sexes (*cf.* fig. 2, crania Nos. 3342 and 3324); while in other instances the difficulty (so marked in the case of the crania of African negro races) of assigning the correct sex to a skull, occurs; (ii.) notice the specimen No. 3324 (*cf.* fig. 1), for besides its generally massive character, it is peculiar in having an erupted and displaced fragment of a tooth on the margin of the nasal aperture. No. 3384 shows a similar condition.

The foregoing (New Britain) specimens may be regarded as typical examples of the Oceanic-negro race.

(d) With the preceding may be contrasted skulls of Polynesian origin as represented by the Kanakas (ref. 2), by the skulls brought by J. S. Gardiner, Esq. (Fellow of Caius College), from the island of Rotuma (see fig. 3, and Nos. 1809–1817), and by the well authenticated series of ten crania of the Mori-ori, a people formerly inhabiting the Chatham Islands, but now practically extinct. It must be admitted that authors are not entirely in agreement as to the affinities of the Mori-ori. The contrast in skull form is one of a series whereby the Polynesians are distinguished from their Melanesian neighbours; it must not be forgotten that many intermediate forms are met with. By taking extremes, the Polynesian skull is distinguished from the Melanesian by its greater capacity, greater breadth, greater parietal eminences, less massive brow-ridges, and higher orbits.

The Polynesian group contains three skulls of Maories, and four crania from Raiatea, but otherwise is not so complete as the Melanesian series. The next specimens worthy of note are three crania from Madagascar (Nos. 1783, 1785), representing two of the cranial forms met with in that island, whereof one is a modification of the skull form commonly found among the Bantu races of Africa (ref. 4). The African skulls will be found on that aspect of this case (No. 3) furthest removed from the door, and comprise examples of ‘West Coast’ negroes, of Kaffirs, of the Bush and Hottentot races of the Cape (ref. 5, 6, 7), of Central African negroes and the specimens

from the battlefield of Tel-el-Kebir. The latter, which we owe to the interest of Messrs Leigh-Smith and Green, of Jesus College, include certainly two crania referable to a negro origin, although others of the series are skulls of Egyptian Fellaheen. The collection of African skulls has been further augmented by the Guanche crania from Teneriffe (ref. 8), and by the enormous collection of crania of inhabitants of Egypt (ref. 12), ancient and modern, which will be mentioned later. But the case under consideration also contains crania from Syria (notice the specimen 1237 for an example of occipital flattening probably of artificial origin, ref. 25), of Jews (probably

FIG. 3.—Native of Rotuma (*Gardiner Coll.*)  
(1814).

from Holland), and a fine series of crania of Punjabis, presented by Dr Havelock Charles, and described by Professor Macalister, assisted by Messrs E. M. Corner and R. J. Horton-Smith (ref. 9).

The two skulls (Nos. 1204 and 1205) from Nagyr in the Gilgit district of Central Asia may be noticed. These rare specimens were obtained by Sir W. M. Conway during his exploration of the mountain peaks of the Himalaya and Hindu-Kush (ref. 10). They are of undoubtedly Caucasian type, and present no trace of Mongolian features; herein they afford contrasts with cranial forms to be met with further east, *e.g.*, in Ladakh, and in Eastern Turkestan (*cf.* a skull from the Macartney collection deposited in this Museum). Lastly, a skull from Kamschatka may be referred to as exemplifying a race but seldom represented in collections (*cf.* ref. 18). Case No. 4 is entirely occupied by Egyptian crania, among which will be found representatives of the inhabitants of Egypt under the Dynasties v. and xviii., also of the date of the Roman occupation, and lastly Egyptians of modern times. For these specimens the University is

indebted to Professors Budge and Flinders Petrie, as well as to F. W. Green, B.A., of Jesus College. The whole series has for some time past been under examination by Professor Macalister, though the results of the investigation have not yet been made available. The example of Egyptian cranium, represented in fig. 4, exemplifies the condition known as scaphocephaly, since the cranial vault is here found to have assumed a keel-shaped or scaphoid form.

The contents of the long case (No. 5) running down the centre of the Museum are a number of skeletons, of which those of aboriginal Australians (at the end nearest the window) are noteworthy, No. 25 showing the form of pelvis (compressed laterally) met with in

FIG. 4.—Egyptian.

males of this race. With this pelvic form may be contrasted that of the Eskimo woman (No. 1873). The origin of the two skeletons of individuals of the Bush race of South Africa is not exactly known, but they present features not altogether typical of that race (for the skulls of which *cf.* specimens No. 1738 *et seq.* in case No. 3). Of the remaining skeletons that of Madame Barré<sup>1</sup> is worth notice; then follow skeletons of East Anglians from near Cambridge (ref. 16), and lastly a most valuable specimen—viz., the skeleton of an individual of the Long Barrow race, which is referred to the Neolithic period in this country. This skeleton forms part of the well-known Thurnam Collection, which was secured for the University by Professor Humphry, and which comprises a large series of crania of the inhabitants of Britain from the Neolithic period onwards.

In the case No. 6 will be found another great collection of skulls of Egyptians, chiefly of the periods following: Dynasty xii. (Memphis,

<sup>1</sup> "Madame Barré, a distinguished French lady, who bequeathed her body to me."—Macartney. (Descriptive notes of the Macartney Collection.) This skeleton is therefore evidently not that of Madame Barry, the famous actress of the eighteenth century and rival of Mrs Siddons.

Nos. 1254-1362, Aswān, Nos. 1364-1459, Qurnah, Nos. 1509-1510), and Dynasty xxii. (Balsamum near Dashasheh, Nos. 3141-3258), and with these two or three mummified heads may be observed, *e.g.*, that of a lady with hair of an unusual degree of blondness; those of a physician, and of a priest; as was evidenced by the characters on the wrappings and casings which have been removed.

In the case No. 7 will be found (on the aspect facing the door) the extensive Hutchinson collection of crania of Peruvians (*cf.* fig. 5), of which some (No. 1987) show the effects of cranial deformation in a marked degree. With these are arranged a few prehistoric crania from Jamaica, presenting forms and deformations not unlike the preceding examples. In the same case are a number of crania of the

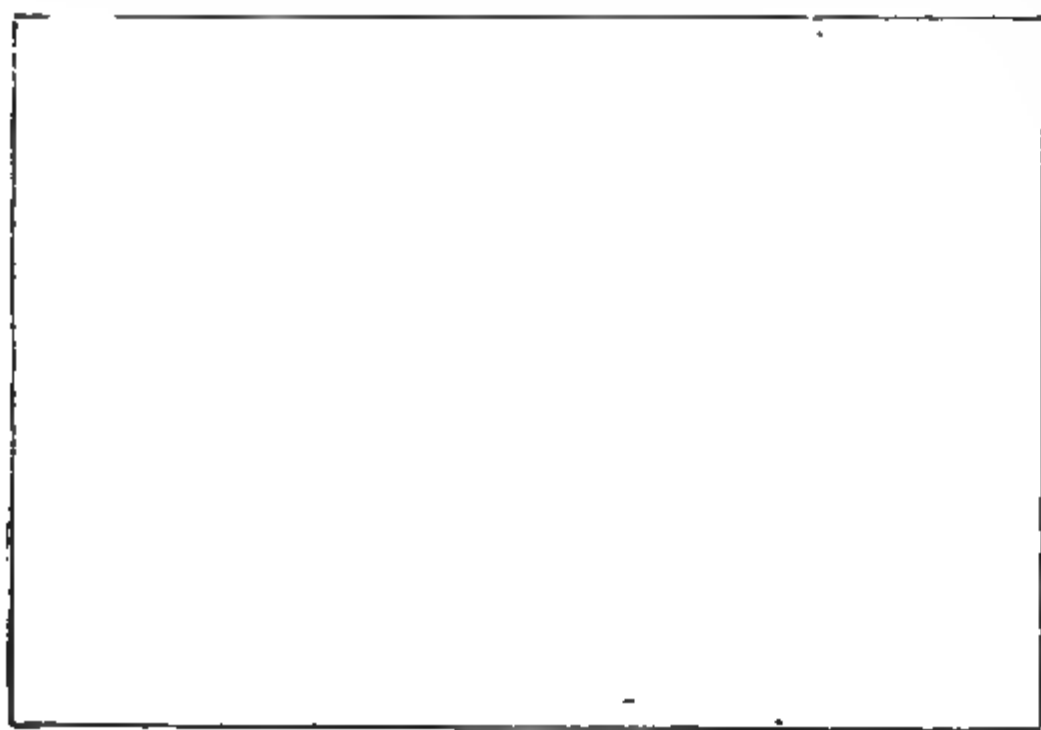


FIG. 5.—Peruvian (*Hutchinson Coll.*).

Eskimo from Greenland and from Labrador, for some of which the University is indebted to Dr Curwen, of St John's College (ref. 13, and fig. 6).

Lastly, there may be noticed a series of crania from Vancouver's Island and British Columbia (which also illustrate the effects of artificial modification of cranial form in infancy), and a few skulls of North American Indians. On the further side of the same case are placed the crania of inhabitants of the British Isles, and here many specimens of the Thurnam Collection will be found (notice No. 551 as an example of the Saxon type of cranium and No. 468 as that of a Briton). These crania may well be considered in connection with the contents of the large wall-case No. 9, in which will be found representatives of several classical epochs in the history of human culture in this land. Thus we find the Long Barrow race (already mentioned as referable to the Neolithic period), with characteristically long narrow skull and countenance. To this succeeds the Round Barrow

race with broad round skull and broader countenance. This becomes merged in the British race of the Roman Conquest, and the latter in the Saxon and Anglian types, to which the crania found at Brandon (and recognisable by the dark brown staining they have received from the soil) seem to be referable as local varieties. A few Saxon crania from Goring will be found in the small wall-case (10) (note No. 666 and *cf.* ref. 14 and 15).

There remain the contents of the wall-case 8, which immediately faces the doorway. This case is devoted to examples presenting conformations that depart from the ordinary or normal type (refs. 19, 20, 21). There may be noticed the presence of a large wormian bone at the lambda (*os incae*, from its supposed confinement to skulls of that race) in both English and Peruvian crania. Division of the malar

FIG. 6.—Esquimaux (1832).

bone is seen in skulls of an East Anglian and a Peruvian respectively. Pressure deformations of artificial origin are seen in the crania of a Vancouver islander, an Avar, and a native of Mallicollo respectively, the latter two being very similar; lastly an example of native trephining may be noticed viz., No. 1904, with which compare the New Britain cranium No. 3340 in case 3.

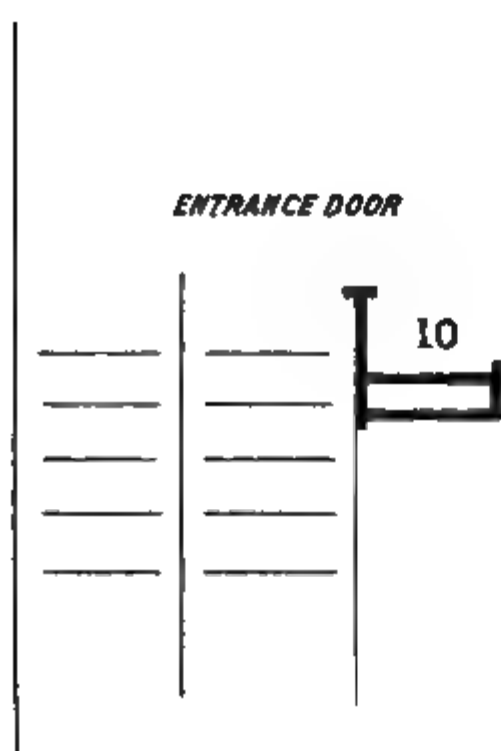
In the end bay case of No. 8 are placed crania of the bathrocephalic, akrocephalic, scaphocephalic, and hydrocephalic varieties; whereof the latter three may be ascribed to defective growth of the cranium, and with these may be compared two examples of microcephalic crania.

Professor Macalister has quite recently completed the arrangement of a new case in the 'Bone-room' of the Museum for the exhibition of specimens illustrating Kollmann's 'types,' and certain cranial abnormalities; of the latter, No. 2286 presents the characteristics of the microcephalic skull in a very marked degree (ref. 17).



PLAN OF MUSEUM OF HUMAN ANATOMY,  
CONTAINING THE  
ANTHROPOLOGICAL COLLECTION.

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It may be repeated, in conclusion, that the present account deals with a mere selection of some of the most interesting of the specimens, which are now numbered by thousands.

# REFERENCES TO DESCRIPTIONS OF SPECIMENS IN THE CAMBRIDGE MUSEUM. (WITH PLAN.)

- (1) AUSTRALIAN ABORIGINES: A Critical Study of Skulls of. W. L. H. Duckworth, M.A., *Jour. of the Anthropol. Inst.*, May 1894, Feb. 1895, Nov. 1897.
- (2) KANAKAS.—Prof. Alex. Macalister, F.R.S., *Jour. of Anat. and Phys.*, Jan. 1898.
- (3) ROTUMA.—J. S. Gardiner, M.A., *Jour. of the Anthropol. Inst.*, Oct. 1898. (Describes how the skulls were obtained.)
- (4) MADAGASCAR CRANIA.—W. L. H. Duckworth, M.A., *Jour. of the Anthropol. Inst.*, Feb. 1897.
- (5) SOUTH AFRICAN CRANIA.—F. Shrubbsall, B.A., *Jour. of the Anthropol. Inst.*, Nov. 1898.
- (6) CRANIA OF BUSH RACES.—F. Shrubbsall, B.A., *Jour. of the Anthropol. Inst.*, 1897.
- (7) CRANIA FROM ASHANTI.—F. Shrubbsall, B.A., *Jour. of the Anthropol. Inst.*, Nov. 1898.
- (8) GUANCHE CRANIA.—F. Shrubbsall, B.A., *Proc. Camb. Phil. Soc.*, vol. ix. part 3.
- (9) PUNJABI AND BENGALI CRANIA.—Prof. Macalister, E. M. Corner, R. J. Horton-Smith, M.A., *Proc. Camb. Phil. Soc.*, Apr. 29, 1895.
- (10) NAGYR CRANIA.—W. L. H. Duckworth, M.A., *Jour. of the Anthropol. Inst.*, Nov. 1893.
- (11) MOOR CRANIA FROM CEYLON.—E. M. Corner, M.A., *Jour. of Anat. and Phys.*, July 1898.
- (12) EGYPTIAN CRANIA.—W. S. Melsome, M.D. (unpublished).
- (13) ESKIMO CRANIA.—W. L. H. Duckworth, M.A., *Jour. of the Anthropol. Inst.*, Aug. 1895.
- (14) SAXON CRANIA.—R. J. Horton-Smith, M.A., *Jour. of the Anthropol. Inst.*, Nov. 1896.
- (15) BRANDON CRANIA.—C. S. Myers, B.A., *Jour. of the Anthropol. Inst.*, Nov. 1896.
- (16) EAST ANGLIAN SKELETONS.—W. L. H. Duckworth, M.A., *Camb. Ant. Soc.*, 12th Feb. 1894.
- (17) MICROCEPHALIC CRANIUM.—Rev. C. Kempson, M.A., *Jour. of Anat. and Phys.*, Jan. 1898.
- (18) CRANIUM FROM KAMSCHATKA.—Prof. Macalister, *Jour. of the Anthropol. Inst.*, 1887.
- (19) DIVIDED PARIETAL BONE.—E. Barclay-Smith, M.D., *Jour. of Anat. and Phys.*, vol. xxxiii.—*Proc. Anat. Soc.*, p. xxiv.
- (20) MALAR BONE EXHIBITING INTRA-JUGAL ARCH.—E. Barclay-Smith, M.D., *Jour. of Anat. and Phys.*, vol. xxxii.—*Proc. Anat. Soc.*, p. xl.
- (21) PLAGIOCEPHALIC EGYPTIAN SKULL.—E. Barclay-Smith, M.D., *Jour. of Anat. and Phys.*, vol. xxxii.—*Proc. Anat. Soc.*, p. xxvi.
- (22) ABNORMAL CERVICAL VERTEBRÆ.—A. S. Grünbaum, M.D., *Jour. of Anat. and Phys.*, vol. xxv.
- (23) PARAMASTOID PROCESSES.—A. S. Grünbaum, M.D., *Jour. of Anat. and Phys.*, vol. xxv.
- (24) SEPARATION OF OS STYLOIDEUM.—E. Barclay-Smith, M.D., *Jour. of Anat. and Phys.*, vol. xxvii.—*Proc. Anat. Soc.*, p. xxxvii.
- (25) SKULL FROM DAMASCUS.—W. L. H. Duckworth, M.A., *Jour. of the Anthropol. Inst.*, Aug.–Nov. 1899 (figs. of No. 1237).

(7) Dr BARCLAY SMITH exhibited a representative collection of the *Works of Early British Anatomists*, supplying, at the same time, the following list, with notes:—

1. "Compendiosa totius Anatomiae delineatio." Thos. Geminus. London, 1559. A scarce and very valuable book. The very excellent copperplates are reproductions of von Calcar's drawings in illustration of Vesalius' Anatomy, of which the book is largely a transcript. (Lent by the Univ. Lib., K. 7, 15.)

2. "A most excellent and learned Woorke of Chirurgerie, . . . and in the ende a compendious worke of Anatomie." John Halle. London, 1565. The expostulation to students in verse is worthy of note. (Lent by the Univ. Lib., K. 10, 54.)

3. "A profitable treatise of the Anatomie of man's body." Thomas Vicary. London, 1577. This is the second edition. The first edition was published about 1548, but a copy of it has yet to be found. (Lent by the Univ. Lib. Adams 8, 57, 7.)

Geminus, Halle, and Vicary were, with the exception of the section dealing with the subject in the 'De proprietatibus rerum' of Bartholomæus Glanville, the first anatomical works published in England.

4. "Microcosmographia." Helkiah Crooke. London, 1618. A rare book. Crooke's anatomical descriptions are not only original in their treatment, but he adds interest to the subject by his entertaining philosophical reflections. (Lent by E. B. S.)

5. "The Englishman's Treasure." Thos. Vicary. London, 1626. (Lent by the Univ. Lib., K. 11, 16.) This is a later edition of the "Profitable treatise."

6. "A description of the Body of man." Alexander Rhead. London, 1634. (Lent by the Philosoph. Lib., L. 12, 14.)

7. "Collegium physicum disputationibus xxxii. absolutum." Franc. Burgerdicius. Cambridge, 1650. Contains a disputation on monsters. *Vide* p. 261. (Lent by E. B. S.)

8. "Corporis Humani Disquisitio." Nathaniel Highmore, M.D. Oxon. Hagæ-Comitis, ex officina Samuelis Brown. Bibliopolæ Anglici, 1651. This was Highmore's first published work, and the only one he wrote dealing with Anatomy, his subsequent writings treating of Hysteria. For description of maxillary antrum, *vide* p. 226, of mediastinum testis, p. 91. (Lent by E. B. S.)

9. "Anatomical Exercises." William Harvey. London, 1653. The first work of Harvey's published in England. A copy of this edition was sold recently at public auction for £40. (Lent by the Univ. Lib., K. 12, 58.)

10. "Microcosmographia." Robert Turner. London, 1654. (Lent by the Univ. Lib., K. 12, 75.)

11. "Anatomia Hepatis." Francis Glisson. London, 1654. (Lent by the Univ. Lib., K. 10, 51.)

12. "Adenographia." Thos. Wharton. London, 1656. For description of duct, *vide* p. 129. (Lent by the Univ. Lib., K. 12, 7.)

13. "De Cordis et Sanguinis Motu." William Harvey. London, 1661. The first edition of this work published in England. (Lent by E. B. S.)

14. "Exercitationes Anatomicae." Robert Bayfield. London, 1668. (Lent by the Univ. Lib., K. 18, 113.)

15. "De Anima Brutorum." Thomas Willis. Oxford, 1672. One of his earliest works. (Lent by Prof. Macalister.)

16. "Tractatus de Ventriculo." Francis Glisson. London, 1677. (Lent by the Univ. Lib., K. 10, 1.)

17. "Exercitationes de differentiis et nominibus Animalium." Walter Charleton. Oxford, 1677. Charleton was a Cambridge man who migrated to Oxford. He served as President of the Royal College of Physicians. (Lent by the Univ. Lib., Hh. 2, 57.)

18. "A description of the rarities preserved at Gresham College, and Comparative Anatomy of the Stomach and Guts." Nehemiah Grew. London, 1681. (Lent by E. B. S.)

19. "Ophthalmographia." William Briggs. Cambridge, 1685. (Lent by the Univ. Lib., K. 12, 76.)

20. "Osteologia Nova." 2nd edition. Clopton Havers. London, 1691. (Lent by the Univ. Lib., K. 11, 7.)

21. "Anatomy of Humane Bodies epitomised." Thos. Gibson. London, 1694. 2nd edition. The first edition was published in 1682 anonymously. (Lent by the Univ. Lib., K. 10, 3.)

22. "Anatomy of the Brain." H. Ridley. London, 1695. (Lent by the Univ. Lib., K. 10, 20.)

23. "Myotomia Reformata." William Cowper. London, 1694. 1st edition. (Lent by Prof. Macalister.)

24. "Essays of Anatomy." Beddevole. London, 1696. (Lent by the Univ. Lib., K. 12, 53.)

25. "Myographia Nova." John Browne. London, 1697. 2nd edition. First edition published 1684. Browne was surgeon to William III. and to St Thomas' Hospital. In the preface he states: "I am obliged to take notice of a rude reflection made upon me and my first book by one Mr Cowper who has wrote somewhat on this subject, who in his preface is pleased to stile it a most erroneous collection of other men's mistakes. . . . I have taken all imaginable care to *imitate Nature in my figures* so far as can be expressed by art, and am not ashamed to say that this design of mine is new and therefore no ways borrowed from any other hand, etc." Cowper (*vide* No. 34) had apparently full justification for his strictures, for if Mr Browne's plates be compared with those of Julius Casserius (*vide* No. 25), it is obvious that the former are bad copies of the latter, though modified either by the side of the body to which the part belongs being reversed, or by alteration of the surrounding landscape, or by some slight change in position. As far as can be seen the only claim which Browne can make to originality rests on the fact that he engraved the names on the muscles themselves instead of indicating them by reference letters. In his elenchus of authors consulted, he veils the name of Casserius under the title J. C. Placentinus. Browne, however, seems to have acquired some considerable reputation on the strength of this work, as it was published at Leyden in 1687 and 1693. Further, it was translated into German and annotated by Christ, Maximil., Speners, being published at Berlin in 1704 and at Leipzig in 1715. Also *vide* Conr. Sam. Schwizfleischii. Epistol. arcan., Tom. 1, p. 58, "Brown medicus est omni exceptione major, cuius historia musculorum nihil accuratius exiit in lucem, adeo, ut Bartholini auditores obstupescerent cum eum virum audirent differentem." It is hardly conceivable that the author of the above can have been acquainted with the beautifully executed plates of Casserius. (Lent by E. B. S.)

26. "Spigelius." Amsterdam, 1645. Containing the plates of Julius Casserius for comparison with No. 24. (Lent by E. B. S.)

27. "The Anatomy of Humane Bodies." Will. Cowper. Oxford, 1698. (Lent by the Philosoph. Lib., B. 2, 11.)

28. "Orang-Outang, or the Anatomy of a Pygmie." Edward Tyson. London, 1699. (Lent by the Philosoph. Lib., E. 2, 55.)

29. "Glandularum quarundam nuper detectarum Descriptio." William Cowper. London, 1702. This is Cowper's original description of the glands associated with his name. The work is interesting, as it contains (p. 21) a letter written by Cowper to Bidloo (*vide* No. 34) full of vituperative sarcasm. (Lent by E. B. S.)

30. "Anatomy of the Humane Body." James Keill. London, 1703. 2nd edition. (Lent by the Univ. Lib., K. 12, 50.)

31. "Anthropologia Nova." James Drake. London, 1707. Drake was in turn playwright, politician, pamphleteer, and anatomist! (Lent by the Univ. Lib., K. 10, 10.)

32. "Anatomy of the Humane Body." W. Cheselden. London, 1722. 2nd edition. (Lent by Prof. Macalister.)

33. "Anatomy improved and illustrated with regard to the uses in designing, demonstrated from the most celebrated antique statues in Rome." Under the care of Chas. Errard. The dissections by Bero. Genga. Explanations by Lancissi. First published at Rome by Dom di Rossi, and now re-engraved and republished by John Senex. London, 1723. (Lent by E. B. S.)

34. "Myotomia Reformata." William Cowper. London, 1724. 2nd edition. The first edition (*vide* No. 23) was published in the author's lifetime. This, the

2nd and more sumptuous edition, was published under the editorship of Richard Mead. This is the Mead who animadverted on Browne's "Myographia Nova." In the preface (p. 6) occurs the following: "That many that have lately written on this subject, especially our English writers, have rather increased than diminished former errors, and particularly that treatise of Mr William Molins and that most erroneous one of John Browne, are chiefly collections of the mistakes of others." Cowper, however, was scarcely in a position to criticise Browne, as he himself was a plagiarist of the deepest dye, cribbing without compunction from Bidloo, to such an extent that the latter wrote a letter to the Royal Society complaining of the treatment he had received at his hands. Also *vide* No. 29. (Lent by E. B. S.)

35. "Osteographia." William Cheselden. London, 1733. This is the first edition. It is remarkable for the excellence of its type and of its plates, probably the finest ever used for a work on Anatomy. In the preface Cheselden states: "This volume was offered by subscription at four guineas, with a promise that none should be sold afterwards for less than six. . . . This volume is made above twenty per cent. better than the subscription proposal. There are no more printed in English than three hundred, . . . the plates shall be destroyed that the price of the book may never sink in the possession of the subscribers." It met with severe criticism at the hands of John Douglas, who published "Animadversions on a late published book entitled Osteographia" in 1735. (Lent by E. B. S.)

36. The MSS. Note-book of a Student. 1734. Copiously illustrated with drawings, chiefly pen and ink, remarkable for the boldness of their execution and the artistic excellence displayed. (Lent by E. B. S.)

37. "Medicina Gymnastica." Francis Fuller. London, 1740. (Lent by the Philosoph. Lib., L. 10, 42.)

38. Knapton's Edition of Albinus. London, 1749. (Lent by Prof. Macalister.)

39. "Compendium Anatomico-medicum." Charles Collignon. Cambridge, 1756. Contains synopses of his lectures. Collignon was Professor of Anatomy at Cambridge, 1753-1785. (Lent by the Univ. Lib., V. 10, 7.)

40. "Medical Commentaries." William Hunter. London, 1762. Interesting, as it contains the account of Hunter's dispute with Monro of Edinburgh regarding priority for the description of the testicular lymphatics. (Lent by E. B. S.)

41. "Myographiæ Comparatæ Specimen." J. Douglas. London and Edinburgh, 1763. (Lent by the Philosoph. Lib., L. 14, 33.)

42. "An enquiry into the structure of the Human Body." Chas. Collignon. Cambridge, 1764. The gift of the author. (Lent by the Univ. Lib., V. 11, 65.)

43. Complete Edition of Harvey's works, edited by the College of Physicians, London, 1766. (Lent by E. B. S.)

44. "A practical treatise on Wounds, etc." B. Gooch. Norwich, 1767. In 3 vols. In Vol. II. may be found a fairly good *résumé* of the rise, progress, and present state of Anatomy. (Lent by E. B. S.)

45. "De anima medica prælectio." A. F. Nicholls. London, 1773. (Lent by the Philosoph. Lib., M. 14, 12.)

46. "The Anatomy of the Human Body." W. Cheselden. London, 1778. 11th edition. (Lent by Prof. Macalister.)

47. "The Anatomy of the Human Body." Sam Foart Simmons. London, 1780. (Lent by the Univ. Lib., V. 14, 62.)

48. "Observations on the Nervous System." Monro. Edinburgh, 1783. Richard Partridge's copy. (Lent by E. B. S.)

49. "Observations on the Nervous System." Monro. Edinburgh, 1783. Sir G. M. Humphry's copy. (Lent by the Philosoph. Lib., B. 4, 9.)

50. "Two introductory lectures delivered to his last course of Anatomical lectures at his theatre in Windmill Street, as they were left corrected for the Press by himself. To which are added some papers relating to Dr Hunter's intended plan for establishing a Museum in London for the improvement of Anatomy, etc." William Hunter. London, 1784. (Lent by E. B. S.)

51. "Observations on certain parts of the animal economy." J. Hunter. London, 1786. (Lent by E. B. S.)

52. "Anatomical Instructor." Thomas Pole. London, 1790. (Lent by the Philosoph. Lib., L. 12, 15.)

53. "A System of Comparative Anatomy." B. Harwood. Cambridge, 1796. Sir Buswick Harwood was Professor of Anatomy at Cambridge 1785-1814. (Lent by E. B. S.)

54. "Anatomy of the Human Body." John Bell. London, 1797. 2 vols. 2nd edition. (Lent by Prof. Macalister.)

55. Abbott's manuscript notes of Abernethy's lectures. A. S. Abbott of St Bartholomew's Hospital. (Lent by Prof. Macalister.)

56. "A System of Dissections." Chas. Bell. Edinburgh, 1798. 1st edition. (Lent by E. B. S.)

57, 58. "Engravings of the arteries illustrating the 2nd vol. of the Anatomy of the human body (J. Bell)." Chas. Bell. London, 1801 and 1811. 1st and 3rd editions. In preface to 3rd edition (p. vii) Bell states: "I have added some other plates, and I have etched most of the plates with my own hand, preferring accuracy to elegance. I have often had to regret in the former editions of my work that my intentions were entirely mistaken by the publishers and artists employed." (Lent by E. B. S.)

59. "Anatomy of the Brain explained in a Series of engravings." Chas. Bell. London, 1802. (Lent by Prof. Macalister.)

60. "A Series of Engravings explaining the course of the Nerves." Chas. Bell. London, 1816. 2nd edition. (Lent by E. B. S.)

61. An original sketch by Chas. Bell. (Lent by Prof. Macalister.)

62. "A Treatise on Ligaments." Bransby B. Cooper. London, 1825. Lecturer on Anatomy at Guy's and nephew of Sir Astley. (Lent by E. B. S.)

Univ. Lib. = Library of the University of Cambridge.

Philosoph. Lib. = Library of the Cambridge Philosophical Society.

(8) Dr BARCLAY SMITH also gave a demonstration on the *Brains, Skulls, and Pelves of two Scaphocephalic Individuals*. This communication will appear at length in the *Journal of Anatomy and Physiology*.

(9) The PRESIDENT exhibited a large collection of *Bones of Ancient Egyptians*, illustrating the prevailing types of their skeletal abnormalities.

(10) Professor A. M. PATERSON read a paper *On Perforations of the Parietal Bones, with exhibition of Specimens*. This communication will be published in full in the *Journal of Anatomy and Physiology*, January 1900.

In the discussion which followed, it was generally agreed that the author was right in regarding such perforations as congenital formations, but it was also held possible that some of them were formed quite late in life.

(11) Dr HANS GADOW, F.R.S., made the following communication *On the Nature of Intercalated Vertebrae of Sharks*:—

The vertebral column exhibited is that of a large specimen of the basking shark (*Selache maxima*), about 10 feet in length. Counting from the head tailwards there are up to the front end of the 43rd chordal block in all 42 axial blocks or so-called vertebral centra, and 42 apparently complete vertebrae, but only 40 neuromeres. The specimen has all the appearance as if two extra vertebrae,

namely, the 31st and the 41st, had been intercalated. But by studying the amplitude of the variations of the dorsal cartilaginous arcualia (basidorsals, interdorsals, and supradorsals), their size, and the way in which they are packed, we can reconstruct the whole vertebral column. Block 41, with its superimposed cartilages, in spite of its resemblance to a complete scleromere, is not one in reality, but is only the enlarged posterior half of a scleromere, and the supposititious scleromere 31 is likewise only the caudal or posterior cadyment of 30. Instead of being partly found with each other, or being partly suppressed as in the first 29 metameres, some of the scleromeres in the transitional region between trunk and tail, have assumed conditions which prevail regularly in the tail of Elasmobranchs. Each complete caudal vertebra, namely, consists of two hemivertebræ, an anterior and a posterior half, hence the muddled conception of 'diplospondyly.' Although the composition of the vertebral column of Elasmobranchs is much less complicated than that of the higher Amniota, cases like the present one are of great value, since they enable us to properly understand how the erroneous doctrine of 'intercalation of vertebræ' is supported, and how it has to be defeated.

(12) Dr ELLIOT SMITH made a *Preliminary Communication on the Morphology of the Cerebral Commissures of Mammals*. This communication will be published at a later date.

(13) The SECRETARY read for Professor J. SYMINGTON a *Note on the Thymus of the Koala*, which will appear in the *Journal of Anatomy and Physiology*, January 1900.

(14) Dr W. H. GASKELL, F.R.S., gave a preliminary account of experiments undertaken to determine the nature and connections of *Giant Nerve Fibres in certain Fishes*. The experiments so far had yielded indecisive results.

(15) Dr CHARLES J. PATTEN exhibited a number of lantern slides, illustrating the *Form and Position of the Thoracic and Abdominal Organs in the Lemur*. The communication dealt chiefly with the position of the viscera in relation to the vertebral column. Compared with those of man, they occupy a lower level. They differ in this respect from the viscera of some of the higher apes (orang and gibbon), which more closely resemble the condition maintained in the newly-born infant. The inner surfaces of the lungs show very distinct impressed areas for neighbouring structures. The aortic groove is even more strongly developed than in the human lung. The trachea and œsophagus in the thorax occupy distinct grooves behind the hilum, the trachea impressing the right lung, the œsophagus the left. The positions of the main fissures of the lungs compared with those of some other groups of animals, were indicated in a tabular form. The heart shows comparatively few peculiarities. The right



L.L.

R.L.

FIG. 1.—Inner surface of lungs, showing depressed areas.

L.L., Left lung.

a.a., Aortic groove.

aes., Esophageal groove.

h., Depression for heart and pericardium.

f., Depression for fat.

b., Base of lung.

R.L., Right lung.

t., Tracheal groove.

r., Root of lung.

h., Depression for right auricle and pericardium.

f., Depressions for fat, with thymic elements.

b., Base of lung.

FIG. 2.—Showing the form of the duodenum (*D*), spleen (*S*), left kidney (*L.K.*), right kidney (*R.K.*), and pancreas (*P*).



auricle is nearly double the size of the left. The conus arteriosus is well marked, forming a distinct oval bulging at the root of the pulmonary artery. The precaval vein, together with the great arterial trunks arising from the aortic arch, are of considerable length.

*Abdominal Organs.*—Of these the most remarkable is the spleen. This is an elongated, crescent-shaped organ, tucked round the outer convex border of the left kidney. The lemurian spleen much more resembles the quadrupedal form than that of higher apes. The kidneys

. 4

FIG. 3.—Mesial section through the male pelvis of the Lemur.

|                                |  |                        |  |                             |
|--------------------------------|--|------------------------|--|-----------------------------|
| <i>R.</i> , Rectal pouch.      |  | <i>P.</i> , Prostate.  |  | <i>A.</i> , Anus.           |
| <i>B.</i> , Bladder.           |  | <i>U.</i> , Urethra.   |  | <i>Ur.</i> , Ureter.        |
| <i>S.v.</i> , Seminal vesicle. |  | <i>S.</i> , Symphysis. |  | <i>V.d.</i> , Vas deferens. |

are proportionately small, the left occupying a lower level than the right. The duodenum is of considerable length, and L-shaped, consisting of a longer vertical part and a shorter transverse part. The latter crosses the spine as low as the 4th lumbar vertebra.

*Pelvic Organs.*—In the ♂ the seminal vesicles are remarkable for their large size. Each consists of a coiled mass, occupying about three turns of a spiral. The bladder very closely resembles that of the human foetus, both in position and form. The rectal pouch in both the male and female is very evident. In the ♀ the short



coiled fallopian tubes were described, also the position of the uterus (bicornuate in character), the single part of which occupies the middle line of the body. The lemurs, before being dissected, were hardened with formalin to ensure the preservation of the accurate form of the viscera. [A fuller account of this paper will be published in the *Transactions* of the Royal Academy of Medicine in Ireland—Section of Anatomy, 1899.]

(16) Mr N. BISHOP HARMAN read a paper on *The Palpebral and Oculo-motor Apparatus of Fishes*, illustrated by lantern and microscope slides.

The work extended over seventy species of fishes.

1. The variations in the simpler forms of palpebral provision, the extra palpebral folds, or pseudo-nictitating membranes, of salmon, herring, etc., were described. The morphology of the nictitating membranes of Selachians was discussed, and the presence of this structure in the Scyllium and its working in the living fish described. The development of the membrane from the ocular surface of the previously formed lower lid was shown in the *Mustelus*, and the development of the musculature of the eyelids of these fish from the musculature of the first gill (spiracle) traced. The existence of an inverse ratio between the state of the spiracle and nictitating membrane was shown.

2. In the relation of the bulb to the ocular walls, the form and variations of an orbital sac, a capsule of Tenon, and such supporting structures as the 'cartilago sustentaculum oculi,' 'ligamentum tenaculum oculi,' and their development were described.

3. Some variations from the normal scheme of the extra-ocular muscles, and provision for projection and retraction of the bulb in certain fish were described. The origin of the recti muscles of the *Zygæna* was shown to be from the basis cranii by means of a long common tendon, and not, as usually considered, from the cranium directly. In the pleuronectids the presence of a specialisation of the superior oblique muscle affording distinct rotatory movement to the eye was described, and the occurrence of some specialisation of this muscle in all cases where convergence of the axis of vision is possible indicated. (The paper was published *in extenso*, with plates, in the *Journal of Anatomy and Physiology*, October 1899, page 1.)

Mr N. BISHOP HARMAN showed *two Livers* from the Cambridge University Dissecting Room, illustrating extreme conditions of the left lobe. Both livers were healthy. Preservative-formalin (figs. 1 and 2).

1. Female, æt. 23. The left lobe is very large, and passes across the median line (*m.l.*), between the diaphragm and spleen, to reach the tenth costal cartilage of the left side in the posterior axillary line. The under surface of the extended left lobe presents a large concavity which receives the greater part of the spleen. The spleen and liver together form an almost symmetrical mass occupying the upper part of the abdomen.

2. Male, æt. 81. In this case, that part of the liver which extends to the left of the median line is very small, being merely a slender triangular mass within the left lateral ligament. This condition is due rather to a displacement than a deficiency of the left lobe, which is compressed so as to occupy a position inferior to the right lobe. Its inferior surface presents one large concave impression which is in contact with the stomach. The attenuated anterior edge is coincident with the costal margin and but slightly bridges the costal angle. The dome of the right lobe is placed abnormally high,

2

*m.l.*, median line; *o.n.*, oesophageal notch; *sp.*, spleen; *i.sp.*, *i.g.*, *i.r.*, *i.c.*, splenic, gastric, renal, and colic impressions respectively; *g.*, gall bladder; *l.l.l.*, left lateral ligament.

reaching to the lower border of the fourth rib in the mid-axillary line. The whole appearance of the organ is that of a short cone.

Although these livers differ so much in shape, there is a remarkable likeness in their bulk, as indicated by displacement of water, and weight:—

|              | I.        | II.       |
|--------------|-----------|-----------|
| Bulk . . .   | 910 c.cm. | 920 c.cm. |
| Weight . . . | 36 ozs.   | 35 ozs.   |

Such extremes of position must be of considerable interest to the clinical worker.

Mr N. BISHOP HARMAN showed a specimen of *Arteria sacra media*, from which arose the pair of 'fifth lumbar' arteries, the 'lowest lumbar' arteries, and some sacral metameric and visceral branches.

(17) Dr T. H. BRYCE gave a lantern demonstration of the fertilisation and segmentation of ova of *Echinus esculentus*. The micro-photographs, which were very excellent, were taken from Dr Bryce's preparations by Dr J. H. Teacher, Assistant to the Professor of Physiology in the University of Glasgow. They were shown in two complete series—(1) of the entire ova magnified 200 D.; (2) of the stages of fertilisation and divisions of the nucleus magnified 700 D. A fuller account of this demonstration will be published.

(18) Dr ADDISON showed the Figures and Tables illustrating his work *On the Topographical Anatomy of the Abdominal Viscera in Man*, consisting of:—

A series of forty plates, showing the abdominal viscera on the life-size scale from forty consecutive cases, also showing in each case the lines of the peritoneal attachments, the various surface and bony landmarks, and the lines used to mark out the regions of the abdomen.

A series of printed tables giving the detailed surface measurements and various descriptive details of each individual case.

A series of six tables, constituting an appendix, giving the precise measurements of all the abdominal viscera from each of the forty cases in regard to one another, to the surface lines, and to the different bony and other landmarks.

Also the following figures:—

Fig. 1. Showing the surface lines in their average position.

Fig. 2. Illustrating the variations of the superficial and deep points in regard to the surface lines.

Figs. 3 A and B. Showing the average position of the abdominal viscera, and the lines of the peritoneal attachments from the whole series of cases. Life-size.

Fig. 4. The stomachs of the forty cases on the scale of 1/9" in relation to the costal arch, the middle line, and the upper transverse abdominal line.

Figs. 5, 6, 7 and 8. Illustrating various points in connection with the stomach bed, and the displacing power of the stomach on the parts behind it.

Fig. 9. Showing the livers of the whole series on the 1/9" scale on the plan of fig. 4.

Figs. 10, 11 and 12. Curves illustrating different points in con-

nection with the movements, the position and relations of the stomach and adjoining viscera.

Figs. 13 and 14. Showing the duodenum and the adjoining viscera on the 1/9" scale, after the manner of figs. 4 and 9.

Fig. 15. Illustrating the variations in the position and relations of the duodenum and pancreas, and the right kidney.

Figs. 16, 17 and 18. Illustrating certain abnormalities of the duodenum.

Fig. 19. Illustrating the duodeno-jejunal folds and fossæ.

Figs. 20, 21, 22 and 23. Illustrating the direction of the chief coils of the small intestine.

Fig. 24. Illustrating various points in connection with the position of the vermiform appendix, and the folds and fossæ in the ileo-cæcal region.

Fig. 25. Showing the arrangement and varieties of the meso-sigmoid.

Figs. 26 A, B, and C. Showing the large intestine and the lines of the peritoneal attachments on the 1/9" scale in relation to the superficial and deep parts, and to the surface lines. (For figs., see *Journal of Anatomy and Physiology* for July and October 1899.)

(19) The PRESIDENT gave the results of an investigation of the cephalic index curves of one thousand *Egyptian Skulls*.

Mr LOCKWOOD's paper on the lymphatic system of the *Appendix vermiformis*, the communications of Mr Higgins on the movements of the *Knee-Joint*, and of Professor Birmingham on specimens illustrating the structure of *Organs of Digestion*, were held over.

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PROCEEDINGS OF THE  
ANATOMICAL SOCIETY OF GREAT BRITAIN  
AND IRELAND.

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NOVEMBER 1899.

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THE First General Meeting of the Society was held at the London School of Medicine for Women, Hunter Street, W.C., on Friday, November 17th, at 4 P.M. In the unavoidable absence of the President, Professor A. MACALISTER, Mr C. B. LOCKWOOD, Vice-President, occupied the chair. Nineteen members and seventy-eight visitors were present.

The minutes of last meeting were read and confirmed.

The Treasurer's Account for the year ending November 1899 was submitted, showing an expenditure of £62, 17s. 8d., and a balance in hand of £63, 13s. 6d. Professor THANE moved and Mr J. BLACK seconded its adoption, which was carried unanimously.

The following candidates were elected members:—JAMES F. GEMMILL, Lecturer in Embryology, University of Glasgow, proposed by A. Macalister, E. Barclay Smith, N. Bishop Harman. ALEXANDER MACPHAIL, Senior Demonstrator of Anatomy, University of Glasgow, proposed by A. Macalister, N. Bishop Harman, E. Barclay Smith.

Officers were elected for the ensuing year:—*President*, A. H. Young, M.B. *Vice-Presidents*—A. Birmingham, M.D.; A. W. Hughes, M.D.; B. C. A. Windle, M.D., D.Sc., F.R.S. *Treasurer*—G. B. Howes, LL.D., F.R.S. *Secretaries*—A. Keith, M.D. (England); T. H. Bryce, M.B., F.R.S.E. (Scotland); Ch. Patten, M.D. (Ireland). *Council*—C. Addison, M.D.; R. J. Berry, M.D., F.R.S.E.; J. Black, M.B.; Stanley Boyd, B.S.; D. J. Cunningham, M.D., F.R.S.; A. F.

Dixon, M.B.; E. Fawcett, M.B.; H. Gadow, F.R.S.; Robert Howden, M.B.; C. B. Lockwood; A. Macalister, M.D., F.R.S.; J. Musgrove, M.D.; F. G. Parsons; A. M. Paterson, M.D.; Arthur Robinson, M.D.; Barclay Smith, M.D.; J. Symington, M.D.; G. D. Thane; Arthur Thomson, M.B.; Sir Wm. Turner, M.B., F.R.S.

The following communications were made:—

Mr STANLEY BOYD showed the *injected Heart of an Infant* found among specimens purchased by the School for Women, from the executors of the late Dr Blundell.

The heart showed a normal vena cava superior: also a persistent left duct of Cuvier, taking the usual course, and opening into the right auricle at the usual spot. There was no left innominate vein, and no trace of any transverse communication in its position.

The vessels springing from the heart were normal (see fig. 1).

FIG. 1.

Miss F. A. STONEY, M.B. (introduced by Mr STANLEY BOYD), showed an *Œsophagus with two well-marked Diverticula*. The lower of these was situated on the front of the œsophagus, immediately below the bifurcation of the trachea. It is the size of a small marble; the interior of the diverticulum is greater in diameter than the neck where it opens into the œsophagus; the neck is almost circular,  $\frac{1}{8}$ " across, and smooth-edged (see fig. 2).

An enlarged bronchial gland was situated to the right and above, but quite to the side of the diverticulum; it was adherent to the side, but left the apex of the diverticulum perfectly free from any of the surrounding structures. This gland was also adherent to the right bronchus. The diverticulum consists of the mucous membrane and submucous tissue of the œsophagus; there is no muscular coat over it, the muscular fibres separating at each side at its base.

The upper diverticulum is  $1\frac{1}{2}$ " from the lower. It is situated anteriorly and to the left of the mid-line; it is much shallower, and is



more oval in outline, being  $\frac{3}{4}$ "  $\times$   $\frac{1}{2}$ ". Here all the coats of the œsophagus are present, there being a complete muscular coat over the whole swelling. This diverticulum was perfectly free, no gland being in its immediate vicinity. There was an elongated gland lying  $\frac{3}{4}$ " to the right, but with no connection to the diverticulum.

The mucous membrane of the œsophagus looks as if, here and there, it were superficially scarred and bereft of normal epithelium. Over an area so altered, below and to the right of the main diverti-

FIG. 2.—Miss Stoney's specimen of sacculated œsophagus.

culum, is another very shallow but fairly definite depression  $1\frac{1}{2}$ "  $\times$   $\frac{3}{4}$ " : the wall here seems just beginning to yield. There is also slight yielding at one place in the upper part of the œsophagus.

The right lung was bound down by dense pleural adhesions, while there were slighter adhesions of the left pleura, and also of the pericardium.

Mr G. P. MUDGE exhibited a *Male Dogfish*, having an abnormal external genital apparatus. That on the right side was normal, but on the left the 'clasper' was absent, the pelvic fin was much smaller than the right, and dissection showed that the basi-ptyrgium was only about half the length, and the number of fin rays only half that in the right fin. As far as dissection was able to show, the nerve supply to both fins was normal, but no investigation was possible upon the trophic nerves, owing to the state of preservation of the specimen.

A *Frog's Hind Foot* was also exhibited showing a bony union between the fourth and fifth metatarsals, at a point about a third of the way along their length. The fourth metatarsal is swollen at the

point where it is ankylosed with the fifth, very much in the same way that human bones thicken at the part of union after fracture. By the courtesy of Dr KEITH, *two consecutive human ribs* which had sustained fracture and reunion, were exhibited, and which showed a similar bony bridge uniting the two ribs between the points of fracture.

Mr G. P. MUDGE exhibited a *Frog* in which a variation of the rectus abdominis muscle had occurred. This muscle in frogs is a segmented one, and is composed of five muscle segments separated by very narrow tendinous bands. In the frog exhibited the first two anterior segments are normal, but behind these the muscle segments are much reduced in width, and the tendinous sheet correspondingly increased, so that the muscle is best described as five muscular strips, the last four being separated by very wide tendinous bands.

Mr G. P. MUDGE recorded a case of connection between the systemic and hepatic portal systems in a rabbit (*Lepus cuniculus*). The anastomosis was formed by a vein (*s.p.a.*) which arose from the left ilio-lumbar (*i.l.*) vein, a little way before that entered the post-caval (*p.c.*), and passing forwards over the left kidney joined the splenic

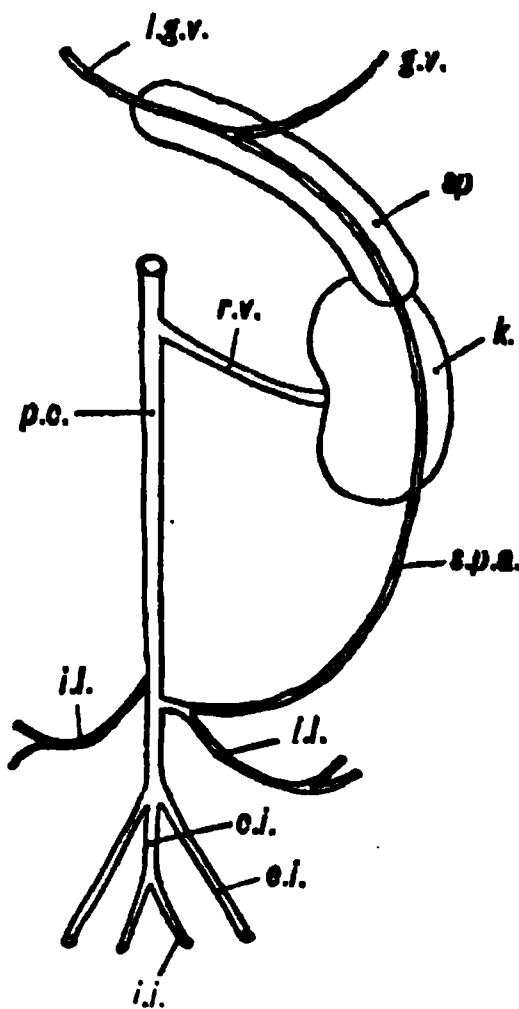


FIG. 3.—*l.g.v.*, lienogastric vein; *g.v.*, gastric vein; *sp.*, spleen; *k.*, kidney; *r.v.*, renal vein; *p.c.*, post-caval; *i.l.*, ilio-lumbar vein; *s.p.a.*, systemic portal anastomosis; *c.i.*, common iliac vein; *e.i.*, external iliac vein; *i.i.*, internal iliac vein.

factor of the lienogastric vein, which subsequently enters the main trunk of the portal vein. Such a connection is very unusual in the rabbit, but in man the two systems are invariably connected by means of the "accessory portal veins" described by Sappey, which form an

anastomosis between the phrenic and azygos veins on the one hand, and the portal vein on the other. Other anastomoses are formed between the left division of the portal vein and veins in the abdominal wall; with the epigastric veins through the par-umbilical veins; and with the vestigial remnant of the embryonic left umbilical vein, or, when that is absent, with the veins related to the round ligament of the liver.

In elasmobranch fishes the hepatic portal system is connected with the systemic by means of two small veins, one of which passes from the lateral line vein to the anterior mesenteric factor, and the other from the posterior cardinal to the same factor of the portal vein.

It cannot be said that the variation described above corresponds exactly to either of the anastomoses in man, amphibians, or elasmobranchs, but it more nearly resembles in its anatomical relations the connection between the two systems formed by the par-umbilical and epigastric veins in the former.

The SECRETARY showed, for Professor PATERSON, the *head of a full-term Fœtus*, in which numerous perforations existed on both sides of the vault of the skull in frontal, parietal, and occipital bones. The perforations corresponded to convolutions of the cerebrum, which at first pressed upon the calvarium, and filled the cavity. The condition was accidentally discovered during the examination of a series of foetal heads, for the purpose of discovering if a vein actually passes through the parietal foramen.

In the discussion which followed, the consensus of opinion was that these perforations were due to localised failures of ossification.

*On the Morphology of the Femoral Head of the Biceps Flexor Cruris.*  
By Professor B. C. A. WINDLE and Mr F. G. PARSONS.

The biceps flexor cruris is a muscle which in quite a large number of mammals is genuinely entitled to the name which it bears—somewhat a distinction among muscles. There are, however, two perfectly distinct and widely different ways in which the structure is two-headed. In the more generalised mammals the heads are ischial and caudal, the latter, which is the more superficial, coming from the anterior caudal vertebræ, and often from the fascia over them; the former, which is deep and not infrequently hidden by the latter, rising from the tuber ischii. The caudal head is often closely connected with the caudo-femoralis (*agitator caule*), and is part of the same plane with that and the ectogluteus. When both heads are present they usually unite fairly high up in the thigh, and are inserted into the patella, the fibula, the tibia, the fascia of the leg, or some combination of these. In many cases a strong prolongation is sent down from the hinder fibres to the region of the heel, where it either fuses with the tendo-Achillis, is inserted into the calcaneum independently, or passes into the sole of the foot with the plantaris.

One of us has already drawn attention to what is, perhaps, the maximum development of the bicipital insertion in *Dolichotis* and *Dasyprocta*.<sup>1</sup>

A double-headed biceps of the ischio-caudal type is met with in many rodents and carnivores.

The rarer form of double-headedness is that in which the heads are ischial and femoral,—a condition which up to the present has only been found in man, in the anthropoids, the platyrrhine monkeys, and the edentates.

In the edentates the condition is a very interesting one, and here, if anywhere, it seemed to us must the key to the riddle of the varying arrangements of the biceps be sought. And when we came to look into the question, our attention was immediately arrested by the fact that the femoral head of the biceps—which is by no means constant in this order—seemed in its absence or presence to bear a very remarkable relation to another muscle, the *tenuissimus* or *bicipiti accessorius*. This muscle is met with in many mammals: thus,

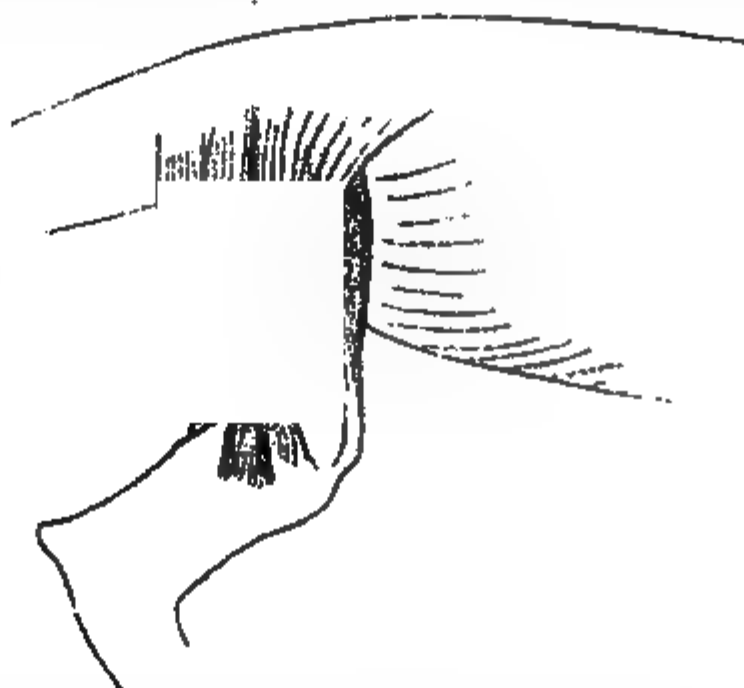


FIG. 4.—Thigh of Lesser Ant eater (*Tamandua tetradactyla*).—*c.f.*, *Ectoglossus* and *Caudo-femoralis*; *B.*, *Biceps femoris*; *T.*, *Tenuissimus* (*Bicipiti accessorius*); *s.t.*, *Semitendinosus*; *Q.*, *Quadriceps femoris*.

for example, it is found among the marsupials in *Dasyurus* and *Didelphys*, though not in *Phascogale*, *Macropus*, or *Petrogale*; it is seldom found among the rodents; it is common among the Carnivora, where it is—as typically elsewhere—a slender ribbon-like muscle which usually rises from the first caudal vertebra, and passes down the back of the thigh and leg, deep to the biceps and superficial to the great sciatic nerve. In the lower part of the leg it usually joins the lowest fibres of the biceps, and, with them, is conducted down to the calcaneum, helping to ensheath the tendo-Achillis. Now let us turn to the consideration of these two muscles, the biceps and tenuissimus

<sup>1</sup> *Jour. of Anat.*, vol. xxi. p. 343.

in the Edentata. Amongst the *Bradypodidae* the femoral head of the former muscle is always present, and the tenuissimus is, we believe, always absent. It is not mentioned by any of the observers who have dissected *Bradypus* or *Choloepus*, and in our dissections of these animals we carefully looked for it, but with a negative result. *Myrmecophaga* has a very interesting second head to its biceps, a head rising neither from the ischium, vertebrae, nor femur, but from the surface of the caudo-femoralis muscle (agitator caudæ), a condition to which we shall have again to refer. *Tamandua* has a typical tenuissimus, but no femoral head of biceps; whereas in all five specimens of *Cyclothurus* of which we have notes, the femoral head was



FIG. 5.—Deep dissection of *Tamandua*. Biceps (B) and Semitendinosus (*s.t.*) cut; *s.m.*, Semimembranosus; T., Tenuissimus.

present, but the tenuissimus absent. The family of the *Myrmecophagidae*, then, which is made up of the three above-named genera, contains examples of both arrangements, and even of a stage intermediate between the two. Amongst the *Dasypodidae* a short head of the biceps has never been found; but in *Dasypus* and *Tatusia* there is a tenuissimus, though not in *Chlamyphorus*, the last member of the family. *Manis* has a femoral head to its biceps, but no tenuissimus. *Orycteropus*, the last form in the Order, has no femoral head to its biceps, but it has a muscle described by Galton as a second part of the semimembranosus, which we have no doubt is really a tenuissimus. The remarkable alternation between these two muscles leads us to think that in them we really have to do with two varying conditions of the same structure; in other words, that the femoral head of the biceps is morphologically a tenuissimus, which has slipped down from its normal attachment to the caudal vertebrae, and obtained an origin from the femur. And here we would again call attention to the intermediate condition described in *Myrmecophaga*, where the caudo-femoralis muscle is apparently acting as a 'muscle-slide' down

which the tenuissimus is creeping to its lower attachment. It is singular that all the conditions should be met with in the one Order, but when we consider how exceedingly aberrant it is in many ways, how reptilian, as Parker has put it, is the variability of its musculature, the fact becomes less remarkable. Passing to the higher forms possessed of a femoral head to the biceps, we are inclined to think that this also may be looked upon as an altered tenuissimus. It is up to man, and even at times in him, a separate or almost separate muscle,

FIG. 6.—Outer side of thigh of Great Anteater (*Myrmecophaga jubata*). *a*, ecto-gluteus; *b*, vastus externus; *c*, caudo-femoralis; *d*, long head of flexor cruris lateralis (biceps); *e*, short head of flexor cruris lateralis (biceps); *f*, semitendinosus; *g*, gastrocnemius.

and then has a lower insertion than the rest of the biceps, and sends down a prolongation to the tendo-Achillis, in all of which respects it behaves like the lower end of a tenuissimus.

In the platyrrhine monkeys it is found in *Ateles*, *Mycetes*, and *Lagothrix*,<sup>1</sup> and it is interesting to notice that it has exactly the same relation to the ischial head of the biceps which it has in the edentates,—that is to say, it crosses the inner (deep) surface of the ischial head, in such a way as to form an X.

In the anthropoid apes the same relationship exists, according to the researches of Hepburn, Keith, and other writers; but now the two heads tend to become slightly fused at their point of crossing.

<sup>1</sup> In *Cebus* it is absent, but we found a delicate tenuissimus.

In man the two parts of the muscle are inserted together, but the femoral head is always internal; and cases are recorded by Hepburn, Macalister, and Testut in which they were separate until their insertion.

*P.S.*—It was our intention to allow the claims of the femoral head of the biceps to be the modified tenuissimus, to rest on the fact that hitherto, as far as we can find out, they have never been found together in any animal, and on the series of intermediate stages which are found between the fully-developed tenuissimus of a generalised mammal, such as an insectivore or carnivore, and the short head of the human biceps. On the nerve supply, our present experience does not lead us to place too much reliance; still, as the members of the Anatomical Society, in commenting upon the paper, evidently laid a good deal of stress on this point, we hasten to incorporate the notes at our disposal. The tenuissimus of a carnivore such as the stoat (*Mustela erminea*), or dog (*Canis familiaris*), is supplied by a branch which comes off from the great sciatic nerve about the middle of the thigh. As Dr Barclay Smith remarked, this nerve can easily be separated into its two popliteal cords, and then the branch to the tenuissimus is seen to come from the external popliteal. In man, the anthropoids and the platyrrhine monkeys (according to Keith), the femoral head of the biceps is supplied by the external popliteal. In the Edentates the tenuissimus or femoral head of biceps, whichever is present, is certainly often supplied by the outer popliteal nerve, or that part of the great sciatic containing the outer popliteal element; but in one specimen of *Manis*, the short head of the biceps was undoubtedly innervated by a branch from the internal popliteal. We would call attention to the fact, that in the kangaroos the radial nerve is a branch of the median, as one instance of the unreliability of nerve paths in determining homologies. Other instances occur to us with which we hesitate to enlarge this paper; but from what we have seen of nerve supplies, we should be very unwilling to regard the femoral head of the biceps of *Manis* as not being homologous with the femoral head of another edentate's biceps, simply because the nerve took a different path to it.

*Note upon the Lymphatics of the Vermiform Appendix.* By C. B. LOCKWOOD, F.R.C.S. Eng., Assistant-Surgeon and Lecturer on Surgical and Applied Anatomy, St Bartholomew's Hospital.

Whilst working at the surgery and pathology of the vermiform appendix, I have met with some features which may interest the Anatomical Society.

But first of all it is perhaps necessary to allude very briefly to the general structure of the appendix. Some seem to be in doubt about the most obvious facts. For instance, Mr Treves speaks of the "so-called muscular coats" of the appendix, and adds that "they are made up . . . mainly of fibrous tissue." Dr Hawkins,

in his admirable monograph, says that the inner *muscular* coat is a stout layer, but the outer is thinner. It would be easy to find other instances of contradictory teaching.

Transverse sections through the normal vermiform appendix are usually 5 millimetres in diameter. The lumen occupies the centre, and may be a mere slit, or the shape of the letter T, or of the letter H, or irregular. Various shapes may be met with in sections through different parts of the same appendix. The coats of the appendix are from 2 millimetres to 2½ millimetres in thickness. Of this the peritoneal and muscular coat are together 1 millimetre thick, the rest being submucosa and mucosa. Beginning from the outside, the appendix is surrounded with a delicate layer of peritoneum, consisting of a layer of endothelium and basement membrane, and of delicate subperitoneal tissue. The latter contains the superficial blood-vessels, lymphatics, and nerves. The outer longitudinal muscular coat is about a quarter of a millimetre thick. Its fibres are irregularly distributed, and may be absent in places. The circular muscular coat is nearly a millimetre thick, and, with the exception of certain gaps, which will be mentioned presently, forms a continuous ring around the appendix. Next comes the submucous coat, which consists of delicate connective-tissue, blood-vessels, lymphatics, and nerves. The mucosa is usually separated from the submucosa by the muscularis mucosæ, which forms the ring at the base of its tubular glands. In an ordinary specimen, from twenty-five to thirty tubular glands can be counted in one section. These are the ordinary Lieberkühn's glands of the large intestine. They are embedded in lymphoid tissue. The lumen of the appendix is lined throughout with a single layer of columnar epithelium upon a basement membrane. In specimens stained with hæmatoxylin or aniline dyes, the lymphoid follicles of the mucous coat are striking objects. They are ovoid, globular, or pyriform bodies 1 millimetre in diameter, and distinctly visible to the naked eye. Some lymphoid follicles are outside the muscularis mucosæ, and are therefore in the submucosa, but most penetrate the muscularis mucosæ, and, displacing the tubular glands, project inwards towards the lumen, where they are covered with columnar epithelium. As a rule, five lymphoid follicles can be counted in one section; but I have counted twelve in a section of the appendix of a girl aged 13 years, sixteen in a man aged 35, nine in a man aged 37, eight in a man aged 36, and five in a man aged 68. The exact number contained in the appendix must depend upon a number of circumstances, especially upon its length and calibre. An appendix of the usual length of 3½ inches contains, at a rough estimate, from 150 to 200 follicles. The substance of each follicle consists of two parts. In the centre is an oval circular area which stands out lighter than the rest, and looks less dense, because its lymph canaliculi are more capacious (*vide* fig. 7). The cortical part of the follicle looks denser and more opaque because of the smallness of its lymph canaliculi. Where the follicle is not bounded by the lymph sinus it merges imperceptibly into the lymphoid tissues of the mucosa, or into that of contiguous follicles (*vide* fig. 7).



One of the most striking features in connection with the lymphoid follicles is the presence of a large lymph sinus, which is shown in the accompanying micro-photograph.<sup>1</sup> This lymph sinus surrounds about half of the circumference of the base of the follicle, and I shall in future refer to it as the follicular lymph sinus or basilar lymph sinus. The narrowest parts of it are crossed by trabeculae. In some forms of appendicitis it becomes dilated and extended, and may completely surround the follicle. In other forms of appendicitis it becomes obliterated either by compression or by accumulation within it of inflammatory corpuscles. The follicular lymph sinus empties itself into the

FIG. 7.—Micro-photograph of normal appendix to show mucosa, lymphoid follicles, and follicular lymph sinus.  $\times 55$ . The lumen is towards the right hand.

lymphatics of the submucosa. This follicular lymphoid sinus has been mentioned by Clado, who, speaking of the appendicular lymphatics, says that they form spaces around the follicles, and are applied like a cap to their deep part. During the summer of 1899, Dr Coffey described them before the Royal Academy of Medicine of Ireland,—at least, so I infer from a brief report of his communication. Similar lymph spaces are depicted by Dr Klein, in his *Atlas of Histology*, at the base of the lymph follicles of a rabbit's cæcum. A drawing of a

<sup>1</sup> The specimens from which these micro-photographs were taken were made for me by Mr Ernest Shaw, and the photographs by Mr Albert Norman. I fear no reproduction could do justice either to the beauty of the sections or of the micro-photographs.

tonsil of a dog in the same work indicates, but less clearly, that the tonsillar follicles possess a basilar lymphatic.

I now propose to show how the submucous lymphatics find their exit from the interior of the appendix. At intervals in the muscular coats certain gaps or hiatus are met with. These gaps are not less than one millimetre wide, and are usually situated at the attachment of the meso-appendix (*vide* fig. 8). At each of these deficiencies in the muscular coat, which I shall in the future refer to as the hiatus muscularis, the subperitoneal and submucous tissues become continuous with one another. The full significance of this continuity of

FIG. 8.—The hiatus muscularis. The inflamed mucosa is at the left, and the meso-appendix at the right. In this section some muscular fibres chance to interrupt the appearance of continuity.  $\times 11$ .

tissue is at once apparent when I state that it is the path by which inflammations which have started in the mucosa reach the peritoneum. It is likewise the path by which bacteria which have attacked the ulcerated mucosa invade the submucosa and peritoneum, setting up various and dangerous forms of septic peritonitis.

The lymphatics of the submucosa penetrate the muscular coats by way of the hiatus muscularis, and after communicating with the subperitoneal lymphatics, pass into the meso-appendix. The subsequent course of the appendicular lymphatics is as follows:—Sometimes they enter the lymphatic gland, which is situated in the meso-appendix at the ileo-cæcal angle. Clado believes that this gland is constant, and

describes and figures it as the appendicular gland. I have not often seen it, because, as Clado says, it may have been concealed by the ileum. From the meso-appendix the lymphatics enter those of the mesentery. The small gland at the ileo-colic angle, and beneath the fossa named the ileo-colic by Rolleston and myself, is constant, and one of the earliest to be implicated in diseases of the appendix. The lymphatics then pass onwards. My own observations are based upon what I have seen in cases of appendicitis. I have so frequently found a chain of inflamed lymphatic glands along the inner side of the right colon behind the ascending meso-colon, that I have come to the conclusion that that is the course which the appendicular lymphatics mainly pursue. Others without doubt open into the mesenteric glands. The lymphatics of the vermiform appendix also empty into those in the iliac fossa along the course of the external iliac artery. They also pass along the appendiculo-ovarian ligament into the right broad ligament of the uterus, and into the lymphatic glands in the right wall of the pelvis in the neighbourhood of the internal iliac artery and vein. I have met with cases of acute appendicitis in which the right broad ligament has been inflamed, tender, and swollen; also a case in which the iliac lymphatics were enlarged, and also with inflammation of the right broad ligament. In a case of carcinoma of the ileo-cæcal valve involving the base of the vermiform appendix, the lymphatic glands along the internal iliac artery were likewise cancerous. There are reasons for supposing that not only may disease of the appendix pass downwards and inwards towards the broad ligament and its contents, but also that infective diseases of the uterus, fallopian tube, or ovary may find their way by the above-mentioned lymph channels to the vermiform appendix.

Clado, in his able memoir, gives the earliest description of the passage of the appendicular lymphatics into the pelvis. Durand has written in confirmation of Clado's observation.

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## FEBRUARY 1900.

A Meeting of the Anatomical Society of Great Britain and Ireland was held at St Mary's Hospital Medical School on Friday, February 2nd, at 4 p.m. The President, Professor YOUNG, was in the chair. Nineteen members and four visitors were present.

When the minutes of last meeting were read it was found that the Hon. Secretary, by an oversight, had omitted to record the Society's vote of thanks to its past President, Professor MACALISTER, for the able way in which he had conducted its business. On the omission being made good, the minutes were duly confirmed.

Professor SYMINGTON gave the results of an investigation (1) on the *Articulations between the Occipital Bone, Atlas, and Axis in some of the Lower Mammalia*. This communication will be published in a future number of the *Journal of Anatomy and Physiology*.

(2) On a Specimen of a Heart with Incomplete Interauricular and Interventricular Septa, one Auriculo-ventricular Opening (left) and a Single Arterial Orifice (Aortic). (See fig. 9.)

Professor SYMINGTON exhibited and read notes of this case of defective cardiac development. The specimen was found in a male child 3 years old, who, since birth, had been cyanotic and suffered from breathlessness, and for about six months before his death had repeated attacks of convulsions. The post-mortem examination was made in a private house, under difficult circumstances, and some of the organs were sent to the pathological department of the Queen's College, Belfast, for examination. Dr Lorrain Smith kindly handed over the heart to Dr Symington. The other organs were apparently free from any malformations, and death was due to tuberculosis.

The heart, when received, was entire and its cavities unopened. The venæ cavæ and pulmonary veins were cut close to the heart, and the aorta was divided through its arch before the origin of the innominate. On the left side of the aorta a vessel was divided which appeared to be a part of the pulmonary artery. The arrangement of the coronary arteries was normal. The coronary sinus occupied its usual position, and the oblique vein of Marshall was almost obliterated.

The auricular part of the heart showed a slight furrow on its

surface, indicating a division into right and left portions. This interauricular groove passed immediately to the left of the inferior vena cava and on the right side of the pulmonary veins. Both the auricular appendices were well developed, especially the left, which was one and a half inches long, and curved forwards on the left side and in front of the aorta. When the heart was opened the two auricles were found to be freely continuous with one another. The common auricular cavity measured two inches from side to side and one inch from before backwards. The imperfect interauricular septum formed a sickle-shaped fold passing forwards from the posterior wall and adjacent portions of the floor and roof. The most prominent part of

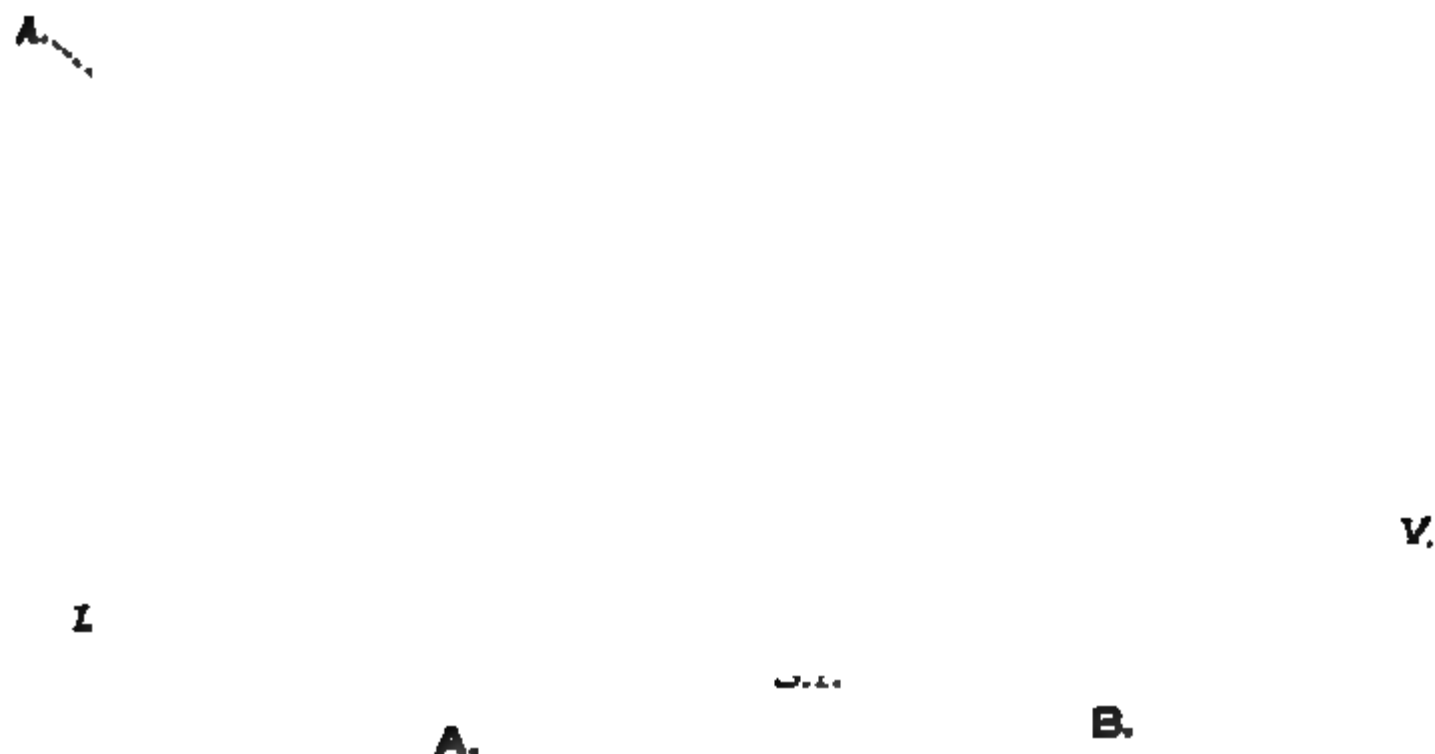


FIG. 9.—Professor Symington's case of Bilocular Heart.

this projection measured  $\frac{3}{4}$  of an inch in height, and the opening between the two auricles readily admitted the index finger. The right portion of the common auricle received the two venæ cavæ and the coronary sinus. The orifice of the sinus was about  $\frac{1}{8}$  of an inch to the right of the interauricular septum, and it had no valve. Musculi pectinati were present in the appendix, and extended backwards and inwards as far as the opening of the coronary sinus. Between the two venæ cavæ and in the neighbourhood of the interauricular septum the walls of the auricle were smooth. There was no trace of a right auriculo-ventricular orifice, and the smooth floor of the auricle was continuous on the left side with the sinus venosus of

the left auricle. The left auricle received two pulmonary veins, one on each side. These openings were perhaps a little smaller than usual, but there was certainly no distinct stenosis. The walls of the left auricle were smooth, except in the appendix, which possessed *musculi pectinati*, and in its floor there was an auriculo-ventricular orifice  $\frac{3}{4}$  of an inch in diameter.

The ventricular part of the heart consisted of a large left and of a much smaller right portion. These communicated with one another by an aperture about half an inch in diameter situated below the aortic orifice. The common ventricular cavity presented only two openings, viz., mitral and aortic; and no traces of the pulmonary or tricuspid could be detected. The ventricle measured 2 inches from the aortic orifice to the apex of the heart, about the same from side to side, and  $1\frac{1}{2}$  inches from before backwards. Its walls varied in thickness from  $\frac{1}{4}$  to  $\frac{1}{2}$  an inch. Its cavity was partially divided into a right and a left portion by a large aortic, or right, cusp of the auriculo-ventricular valve, and by a group of *musculi pectinati* which sprang from the apex and the anterior and posterior walls of the ventricle. The cusps of the auriculo-ventricular valve were three in number; of these the largest was situated on the right side, between the auriculo-ventricular and aortic openings, and was closely related at its base to the left posterior aortic valve. The other cusps were right anterior and right posterior in position. The aortic orifice was on the right side of the auriculo-ventricular. Its valves were three in number, one anterior and two posterior.

The part of the interventricular septum which was developed represented the septum inferius of His. It sprang from the ventricular wall about an inch to the right of and above the apex of the heart, and formed a thick muscular mass with an upper free concave border. This began anteriorly about  $\frac{1}{4}$  of an inch below the anterior aortic cusp, and extended posteriorly upwards close to the interval between the two posterior cusps. A further upward development of this septum would, therefore, have tended to divide the aortic vestibule into two parts, one communicating with the right and the other with the left ventricle.

The right ventricle was much smaller than the left. It formed scarcely one-eighth of the anterior aspect of the ventricular part of the heart, but it was better developed behind, being here fully half the size of the left ventricle. The upper and back part of the right ventricle formed a cul-de-sac, which appeared on the surface as a pointed process lying behind the right auricle. The interventricular aperture admitted the little finger.

It is evident from this description that the heart was physiologically bilocular, for, although the auricles and ventricles were partially divided, the arterial and venous blood had to pass together through the same valvular orifices. This case is a well-marked example of arrested development without the irregularities which are frequently associated with such an extreme case of non-development. The venous sinus of the developing heart had undergone its normal

changes, and the main defect of the auricular portion is due to the incomplete formation of the septum.

According to Born the common auriculo-ventricular orifice in the rabbit is situated at first on the left side. It gradually extends to the right, so that the opening reaches transversely above the septum inferius and opens into both ventricles. In this case the auriculo-ventricular orifice maintained its original position on the left side, and there has been a total absence of the somewhat complicated processes by means of which two distinct auriculo-ventricular openings are formed. In a similar manner the aortic bulb persists, the endocardial septum, which normally divides it into two, not having appeared. In connection with the aortic orifice it is interesting to observe that it possesses three semilunar valves, and not four, as one might expect from the fact that four endocardial cushions are formed at the lower end of the aortic bulb.

Unfortunately the ductus arteriosus and right and left pulmonary arteries were not removed with the heart, so that we do not know their condition, but usually in cases such as this the blood going to the lungs passes from the aorta, *via* the ductus arteriosus, into the pulmonary vessels. The specimen showed an artery lying on the left side of the aorta in the position of the pulmonary artery. On passing a probe down this vessel its lumen was found to terminate blindly a short distance above the heart. Stenosis of the pulmonary orifice and adhesions between the pulmonary valves are often found in specimens of cardiac malformation, but complete absence of the pulmonary orifice and adjacent portion of the pulmonary artery is not nearly so common. The portion of the pulmonary artery present in my specimen was probably developed as a ventral process of the 5th left aortic arch.

(3) Professor SYMINGTON showed, for Dr R. D. RUDOLF (Toronto), *a Case of Cor Biloculare* (see fig. 10). Dr Rudolf sent the following notes:—

“The specimen was some years old when it came into my possession. Dr A. A. Macdonald, who attended the patient, has kindly recorded his recollections of the case as follows:—

B. M., æt. 16, but looks 13 years. A poorly developed girl. Has always been cyanotic and incapable of much exertion. Has been some years in the Protestant Orphans' Home. Family history unknown. She developed pulmonary phthisis, with the ordinary symptoms, which were rendered more distressing by the difficulty of breathing, due to the cyanosis. My recollections of the case are that, though the heart sounds were abnormal, I was unable to make the diagnosis, and that I attributed the cyanosis to non-closure of the foramen ovale.

The heart externally presents very little abnormal appearance. It measures 5 inches from the apex to the roof of the auricle, and  $7\frac{1}{2}$  inches in circumference one inch below the auriculo-ventricular groove. It weighs  $5\frac{1}{8}$  ozs., which is the normal weight of the heart

of a girl of 12 years, but it has been some years in spirits, so no doubt weighs light.

The coronary arteries are normally placed in the position of the inter-ventricular grooves, which are slightly marked. The great vessels were all cut off short, and thus the condition of the ductus arteriosus remains doubtful, but there can be seen the stumps of the aorta, pulmonary artery, superior and inferior venæ cavæ, and of four pulmonary veins.

The left auricular appendix is normal in appearance; the right is enlarged and doubled down upon itself. On examining the interior of the auricles it is seen that the right portion is twice as large as the left. Its floor is completely closed, and thus there is no trace of a tricuspid orifice. There is, however, a shallow fossa here, and a sharp needle passed through the bottom of this in a vertical direction appeared in the posterior wall of the ventricle  $\frac{1}{8}$  inch to the right of the centre of the right auriculo-ventricular cusp, and well within the *left* portion of the common ventricle. Immediately behind this fossa is a well-marked opening of the coronary sinus. This is bounded posteriorly by a thick fold, and anteriorly by a membranous valve. These join to the left of the orifice, and thus form a ridge

FIG. 10.—From a photograph of the Heart described by Dr Rudolf.

which runs towards and blends with the ridge which marks the division between the two auricles. The left auricle is, as stated, relatively small, but otherwise is normal. The opening between the two auricles is almost of the same diameter as the auricles themselves. It is slightly closed by a sickle-shaped membranous ridge  $\frac{1}{8}$  inch in width at its widest part. This ridge lies posteriorly, and its cornua extend along the roof and floor, but there is no trace of it anteriorly.

The walls of the auricles are about  $\frac{1}{8}$  inch thick on the average.

The ventricular cavity is a single one, and at first sight shows no sign of division into right and left portions. On close examination, however, a thick muscular ridge is seen running in a semicircular fashion, so as to suggest such a division. This ridge begins  $\frac{1}{8}$  inch to the right of the right auriculo-ventricular cusp, and runs downwards and forwards to within  $1\frac{1}{2}$  inches of the apex of the heart. It then sweeps upwards and backwards, and ends at the anterior end of the left auriculo-ventricular cusp. The auriculo-ventricular orifice, the



only one, opens thus into the left ventricle, while both the aorta and the pulmonary artery open out of the right ventricle. The inner surface of the common ventricle is occupied completely by columnæ carneæ of the three kinds, *i.e.*, bridges, ridges, and muscoli papillares. There are about twelve of these last named, varying much in size. They are connected by chordæ tendineæ with the cusps of the auriculo-ventricular valve, and it is interesting to note that those connecting with the anterior portions of the cusps arise from the wall of the right ventricle.

The auriculo-ventricular orifice measures 1 inch in its antero-posterior, or largest diameter. It is guarded, as already alluded to, by two cusps placed laterally. These were sufficient to make the orifice competent during ventricular systole.

The aorta, arising from the right ventricle, measures  $\frac{3}{4}$  inch in diameter at its orifice. The valves are three in number, and are situated right, left, and posterior, and the coronary arteries arise from the left and posterior sinuses of Valsalva.

The pulmonary artery itself measures  $\frac{9}{16}$  inch in diameter. It arises posteriorly, and to the left of the aorta. Its orifice is much constricted by a complete fusion of the valves, a funnel-shaped passage being thus formed, which projects into the lumen of the vessel  $\frac{3}{4}$  inch, and measures  $\frac{5}{16} \times \frac{3}{16}$  inch at its opening. The margin of this is fibrous and firm. Two frænæ run from this to the walls of the vessel. One of these is situated anteriorly, and to the right, and the other posteriorly. These suggest the fusion of two valves, of which the larger was the left. The conus arteriosus begins abruptly between the auriculo-ventricular and aortic orifices, but nearer to the former. It measures  $\frac{10}{16}$  inch in its posterior wall, and  $\frac{8}{16}$  anteriorly. Its commencement is a strong fibrous ring, measuring  $\frac{8}{16} \times \frac{5}{16}$  inch. Its inner surface is corrugated.

The wall of the common ventricle measures  $\frac{1}{2}$  to  $\frac{3}{4}$  in thickness, the right side being slightly the thicker.

Thus, to sum up, in this heart there is :—

1. An almost complete absence of the auricular septum.
2.       "                       "                       ventricular septum.
3. A single auriculo-ventricular orifice, which is bicuspid.
4. A transposition of the aorta and pulmonary artery, both of which arise from the right side of the heart.
5. A stenosis of the conus arteriosus.
6. A stenosis of the pulmonary orifice, due to adhesion of the pulmonary valves, of which there were apparently originally only two.

The condition of the ductus arteriosus, unfortunately, as stated, remains uncertain."

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(4) Professor E. FAWCETT gave an account of *Some Anatomical Observations from the Post-mortem Room*, made in conjunction with Dr J. V. BLACHFORD, City and County Asylum, Bristol.

It some years ago occurred to one of us that much valuable information, from the anatomical point of view, might be got from the post-mortem room of the Bristol Lunatic Asylum,—information which would be as accurate as possible, and from the nature of things very uniform.

The first structure that came under our especial notice was the vermiform appendix, and we had much guidance in our examination of this structure in a paper written by Dr Berry of Edinburgh, in 1895, in the *Anatomischer Anzeiger*, entitled "The Anatomy of the Vermiform Appendix."

Dr Berry examined 100 specimens, and from them came to certain conclusions as regards the average length of the appendix, the relation of length to sex, and the relation of appendix to age. He also made observations on the diameter of the appendix, and regards these last observations to be of considerable physiological and pathological importance.

Our observations run much on the same lines as those of Dr Berry, and they are based on an examination of 350 specimens, and we particularly emphasise the statement that all remarks as to length, etc., were entered in a book kept for that purpose *at the time of examination*; and that as the examinations were made about the same time after death, and under similar circumstances, the results are of necessity as uniform as possible. In every case the appendix was measured when in the body.

1. *The Length of the Appendix.*

This we have found to vary from 1·5 to 19 centimetres, but the average length, based on 350 cases, is 8·44 cm. Dr Berry, on his 100 cases, founded an average of 8·3; this agrees with the average of 8·3 obtained by Ribbert on an examination of 400 cases.

Other observers examining fewer cases have, as a rule, obtained a higher figure, as will be seen from the appended table, which we quote from Dr Berry's paper.

TABLE I.—*Combined Average Length of Appendix.*

|                                   | cm.               |
|-----------------------------------|-------------------|
| 1. Clado . . . . .                | 8                 |
| 2. Ribbert . . . . .              | 8·3 (400) cases.  |
| 3. Berry . . . . .                | 8·3 (100) cases.  |
| (Blachford and Fawcett) . . . . . | 8·44 (350) cases. |
| 4. Struthers . . . . .            | 9                 |
| 5. Kelynack . . . . .             | 9                 |
| 6. Fowler . . . . .               | 9                 |
| 7. Bryant . . . . .               | 9                 |
| 8. Smith . . . . .                | 9                 |
| 9. Raushoff . . . . .             | 10·2              |
| 10. Treves . . . . .              | 10·2              |
| 11. Fergusson . . . . .           | 11·5              |

Dr Berry takes the mean of these figures, which is 9·2 cm., one which is more accurate than the ones previously given. After our own observations, taken under the circumstances mentioned above, we cannot but think that 9·2 cm. is too generous an average, 8·3 or 8·4 being much more probably near the mark.

The longest appendix met with by Dr Berry measured 13·3 cm.; we had as many as thirteen measuring 13 cm., and a like number longer than that, up to 19 cm. Ribbert has seen one 21 cm. in length.

The shortest appendix seen by Dr Berry was 3·1 cm., our shortest is 1·5 cm., and we have seen five specimens shorter than 3·1 cm.

According to Dr Berry, "Some authors have described total absence of the appendix. I do not believe, however, that the appendix is ever absent, unless as the result of a previous excision." We have a specimen in our possession which lacks the appendix, likewise any sign of inflammation.

Following on Dr Berry's plan, we now examine the relation of sex to length of the appendix.

TABLE II.—*Relation of Sex to Length of Appendix.*

|                      |                |         |
|----------------------|----------------|---------|
| Dr Berry finds in    |                |         |
| 1. Males . . . . .   | average length | 8·6 cm. |
| 2. Females . . . . . | " "            | 8       |

We have found in

1. Males . . . average length 8.88 cm.
2. Females . . . " " 7.87

Thus, according to our results, the male appendix is 1 cm. longer than the female. This agrees with Bryant's observations.

Kelynack finds in favour of the female appendix by a margin of  $1\frac{1}{2}$  mm.

We agree with Dr Berry in stating that the male appendix is longer than the female.

Still following Dr Berry's lead, we examined the relations of length of appendix to age.

TABLE III.—*Relations of Length of Appendix to Age, based upon an Examination of 350 Cases.*

| From 10-20 years | 9 cases | average 8 cm. |
|------------------|---------|---------------|
| 20-30 "          | 31 "    | 7.7           |
| 30-40 "          | 65 "    | 9.06          |
| 40-50 "          | 66 "    | 8.5           |
| 50-60 "          | 59 "    | 8.66          |
| 60-70 "          | 58 "    | 8.62          |
| 70-80 "          | 49 "    | 7.48          |
| 80-90 "          | 10 "    | 8.8           |
| 90-100 "         | 3 "     | 7.3           |

From this table it would appear that the appendix is longest between the ages of 30 and 40 years. This agrees in the main with Dr Berry's statement that it is longest between the ages of 20 and 40 years.

There is no such gradual diminution here, as has been seen by Ribbert. In fact, the most striking thing to our mind is that three cases (lunatics) have attained an age of 90 or over—one being 95 years of age.

If we next consider the relationship of age and sex to the length of the appendix, we get—

TABLE IV.—*Relationship of Length of Appendix to Age and Sex.*

| Age.             | Cases. | Average,<br>Males. | Cases. | Average,<br>Females. |
|------------------|--------|--------------------|--------|----------------------|
| From 10-20 . . . | 5      | 9·2                | 4      | 6·5                  |
| 20-30 . . .      | 13     | 8·92               | 18     | 6·8                  |
| 30-40 . . .      | 43     | 8·95               | 22     | 9·2                  |
| 40-50 . . .      | 40     | 8·96               | 26     | 7·9                  |
| 50-60 . . .      | 32     | 9·1                | 27     | 8·1                  |
| 60-70 . . .      | 30     | 9·4                | 28     | 7·7                  |
| 70-80 . . .      | 24     | 7·8                | 25     | 7·1                  |
| 80-90 . . .      | 8      | 8·4                | 2      | 10·3                 |
| 90-100 . . .     | 2      | 7                  | 1      | 8                    |
|                  | 197    | 8·8                | 153    | 7·8                  |

It is evident that sweeping conclusions cannot be drawn from these tables.

We next thought that body stature might have some relation to the length of the appendix, and we took in series 100 cases. Perhaps it has as definite a relation to it as age and sex, but that is not saying much. We gave up at 100 cases. The following table, based on 100 cases, shows :—

TABLE V.—*Relation of Stature to Length of Appendix.*

| Body Height. | Average Length of Appendix. |
|--------------|-----------------------------|
| 4' 5½"       | 7 cm.                       |
| 4' 9"        | 5                           |
| 5'           | 10                          |
| 5' 1"        | 12·5                        |
| 5' 2"        | 8·7                         |
| 5' 3"        | 8·1                         |
| 5' 4"        | 9                           |
| 5' 5"        | 9                           |
| 5' 6"        | 8·6                         |
| 5' 7"        | 8·9                         |
| 5' 8"        | 8·8                         |
| 5' 9"        | 9·2                         |
| 5' 10"       | 8·5                         |
| 6'           | 12                          |

The reader may draw his own conclusions from the above table.

Finally, it has been maintained that the appendix tends to become obliterated as age advances. Ribbert makes very definite statements on this point.

Berry also is so definite as to say that, "After, or about middle age, obliteration of the appendix is the rule, not the exception."

We have records of 221 cases, and of these the appendix was pervious in 196—that is, in 88 per cent.

In 133 males it was pervious 114 times, partially pervious 3 times, 16 times impervious. In 88 females it was pervious 82 times, partially pervious once, and obliterated in 5 cases.

Out of the total of 196 pervious cases, no less than 91 were over 50 years of age, many of them well over it—all the nineties were in fact pervious—51 male appendices over 50 years of age out of 114 were pervious, and 40 female appendices out of 88 pervious specimens were over 50 years of age.

The subjoined table expresses these points more clearly.

TABLE VI.—*Obliteration of Appendix.*

|            |   |   |   |              |        |
|------------|---|---|---|--------------|--------|
| 221 Cases  | . | . | . | 196 Pervious | = 88·1 |
| 133 Males  | . | . | . | 114 „        | = 84·9 |
| 88 Females | . | . | . | 82 „         | = 93·1 |

It may be that as part of a general physiological process of atrophy, that the appendix undergoes diminution in calibre, and becomes shorter. We doubt if there is any special atrophy of that organ; at all events, none of the figures we have presented warrant such a sweeping statement.

*General Conclusions—*

1. That the vermiform appendix averages 8·4 cm. in length.
2. That it is 1 cm. longer in the male than in the female.
3. That there is no very definite relation between age and length of appendix—perhaps it is longest between the ages of 30–40.
4. That there is no very definite relation between body stature and length of appendix.
5. That much more conclusive evidence is wanted to show that there is a special atrophy of the appendix in old age or after middle life.

(5) Mr M'ADAM ECCLES showed specimens of *abnormally long Vermiform Appendices*, and said that the length of the vermiform appendix is not only of considerable interest from a purely anatomical point of view, but it is of importance from a pathological aspect. I have therefore ventured to bring before the Society this afternoon two specimens of unusual length of the appendix, each of which was associated with a morbid condition.

The first specimen, which I pass round, is that of an appendix which measured no less than nine inches before it was placed in spirit. It was removed from a man at the West London Hospital by my colleague, Mr C. B. Keetley, on Jan. 23rd, 1900. The patient had had at least two attacks of appendicitis, and it was about ten days

after the subsidence of the last that the abdomen was opened and the appendix removed. The organ was discovered imbedded in adhesions; tortuous, and inclining upwards and to the left behind the lower end of the ileum. The extremity of the tube was tapered, and had passed through a layer of adherent peritoneum close to the mesentery of the ileum. It will be noticed that although it had been the site of inflammation, it does not show any degree of enlargement, thickening, or constriction.

The second specimen is one of hernia of the vermiform appendix. Here, again, the organ is of unusual length, and has passed into the sac of a right femoral hernia, of which it constitutes the sole contents. I apprehend that an appendix of more than ordinary length is more likely to find its way into a hernial sac; but I also think that if it has been so protruded, that there is a possibility of its length being increased by the drag that is likely to be exercised upon it should it become adherent in the sac.

Mr Black said that there was an abdomen now being dissected in the Westminster Medical School, in which the vermiform appendix certainly did not exceed  $\frac{3}{4}$  inch in length. Last winter, in the same dissecting room, there was an inguinal hernia in which the vermiform appendix was the sole content of the sac, to the fundus of which it was fixed by adhesion. Some years ago he saw in the same room a hernia of the cæcum with the vermiform appendix, which was said to be a commoner condition than of the latter only. With regard to the frequency of a patent foramen ovale, Prof. MacAlister gives 33%, which almost precisely corresponded with that given by Prof. Fawcett.

It was interesting to note the bifurcation of the abdominal aorta was stated to occur to the left of the middle line in only 25% of the cases examined, as he had generally been unable to verify the leftward deviation in the course of this great work, although he thought it was usually mentioned in our text-books.

(6) Dr GASKELL read a paper on *The Meaning of the Trigeminal Group of Nerves, and the Relation of the Olfactory Organ to the Old Mouth.*

This paper forms the next instalment of the series of papers on the origin of vertebrates which he has already published in the *Journal of Anatomy and Physiology*, and will form Parts V., VI., VII., VIII.

Part V.—On the origin of the pro-otic segmentation; the meaning of the trigeminal and eye muscle nerves.

The evidence of the number of segments, and the nature of the appendages in the prosomatic region of the Merostomata is given, and it is pointed out how the evidence of anatomists and morphologists as to the segmentation of the trigeminal region of the vertebrate is in harmony with that of the prosomatic region of the Merostomata, as determined by the head cavities, muscle segments, neuromeres, and nerve distribution. The eye muscles supplied by the oculomotor nerve are shown to have been originally the anterior group of dorso-ventral somatic muscles of the prosoma, belonging to the concentrated segments of the endognaths, while the superior oblique supplied by the trochlearis nerve is shown to have been the corresponding dorso-

ventral muscle of the next segment, viz., the segment belonging to the pair of ectognaths. By the crossing of this muscle over the mid-dorsal line the position of the trochlearis nerve is explained after the method of explanation put forward by Fürbringer. The external rectus is the foremost mesosomatic dorso-ventral muscle, which has been pressed into the service of the eye.

Part VI.—The old mouth and the olfactory organ; the meaning of the 1st nerve.

In this part the olfactory organ of the Merostomata is considered, and it is pointed out how the camerostome represents the conjoined olfactory antennæ of the crustaceans, and how it absolutely corresponds with the olfactory organ of the Ammocetes. The camerostome forms an olfactory tube, at the end of which the true mouth is situated, leading into the enlarged pharynx. By the simple closure of the mouth, this olfactory tube becomes the hypophysial tube, i.e., the nasal tube of Ammocetes, and the pharynx with the coxal glands in its close neighbourhood becomes the saccus vasculosus with the pituitary body closely attached. Thus the palæostoma of Beard and of Kupffer was originally the mouth of the Eurypterid. The structure of the nasal tube of Ammocetes is shown to correspond closely with that of the olfactory tube of Thelyphonus, and the structure of the pituitary body of Ammocetes with that of the coxal glands of *Limulus*.

Part VII.—On the evidence of prosomatic appendages in Ammocetes. In this part the region supplied by the fifth nerve in Ammocetes is considered in detail, and it is shown how the consideration of the skeletal tissues, the muscular tissues, and the nerve distribution of this region all point to the conclusion that the oral chamber of Ammocetes was formed from the Eurypterid metastomal chamber; and that in the lower lip, the tongue, the tentacles, and upper lip we have the last remnants of the metastoma, the pair of ectognaths, the endognaths, and prosternite of the Eurypterid ancestor.

Part VIII.—The palæontological evidence—Ammocetes a Cephalaspid.

In this part the evidence of the external muco-cartilaginous skeleton of the Ammocetes, together with the changes it undergoes, is considered, and its extent mapped out. This muco-cartilaginous skeleton forms a ventral and a dorsal head-shield of exactly the same shape and character as the dorsal and ventral shields of the Cephalaspidæ, and it is pointed out how all the structures seen in the dorsal shields of these old fishes are the same in character and position as those seen in Ammocetes. Further, the structure of this muco-cartilage is remarkably similar to that of the so-called bone in these ancient head-shields. The conclusion, therefore, is arrived at that Ammocetes is a Cephalaspid, just as must have been the case if, on the theory put forward in this series of papers, the first formed fishes were Ammocetean in nature. The full paper will appear shortly in the *Journal of Anatomy and Physiology*.

(7) Mr EDRED M. CORNER read the following note upon the *Relations of the Ureter* from the point where it crosses the external iliac artery



to where it enters the posterior peritoneal ligament of the bladder. Twenty-five bodies were examined, and the note is only presented in this form as the examinations could be no longer carried out. The ureter crossed the external iliac artery more frequently than the bifurcation of the common iliac. It then came in relation with the external iliac veins. The origin of the common iliac vein is not infrequently distal to the bifurcation of the corresponding artery. In this case the ureter will lie upon the common iliac vein, and then on the internal iliac vein. The ureter then followed successively the anterior border of the internal iliac artery, the anterior border of the anterior branch of the internal iliac artery, the anterior border of the common hypogastric trunk crossing the superior vesical vessels and following the superior border of the inferior vesical artery to the bladder. It was pointed out that the superior, inferior, and uterine arteries seemed to arise successively from the hypogastric trunk, and not as indicated by the diagram in the Report of the Committee of Collective Investigation, 1895-96, p. 14. Some text-books state that the obturator internus is a relation to the ureter, but, as was pointed out, it is separated from it by the planes of the arteries and veins, and deep to these that of the obturator nerve. The obturator artery passes beneath the ureter and the inferior vesical artery.

(8) Mr EDRED M. CORNER read a paper on *The Varieties and Structure of the Patella of Man*, with a comparison with that of a quadruped, of which the following is an abstract:—

The forms of the human patella may be roughly classified into triangular, oblique, elliptical, and circular; the approximate percentages of these forms being 66, 20, 9, and 5 respectively. In the female bone the oblique and elliptical types were more frequently found. On an average the female patella was lighter than the male. No racial characters could be discovered.

The quadruped's patella, owing to the naturally flexed knee, bears a constant strain and is a strong bone, supported by the femur in almost its entire length. In man, the weight being transmitted directly from the femur to the tibia, the patella is largely functionless. It is also a relatively broader and thinner bone, and is not nearly so completely supported by the femur. In connection with the greater strain on the quadruped's patella, it is interesting to note that muscles are inserted into it that are not so in man, *e.g.* the biceps and gracilis (*Journal of Anatomy*, xxxii. p. 737).

On examining a sagittal section of a human patella, it is seen that the anterior surface is composed of compact bone in which the fibres run parallel to the surface. At the upper end of the bone the compact layer originates in a mass of dense bone which corresponds to the main insertion of the quadriceps tendon. Towards the lower end or apex of the bone the anterior compact layer becomes thinner, and practically ends before the apex is reached. On the deeper surface of this layer the fibres become more and more separated from each other, and towards the centre form part of the meshwork.

Next to the articular cartilage is a much thinner layer of compact bone which is thickest in the upper half and gets thinner as the apex

is approached. Its deeper fibres join the central meshwork more quickly than the anterior fibres do.

These compact layers vary much in thickness in different specimens, and, as might be expected, are usually best developed in male patellæ.<sup>1</sup> The longitudinal fibres are by far the best developed in the anterior portion of the bone, and represent lines of traction. It is interesting to note that in this situation the leverage gained from the thickness of the patella has the greatest mechanical advantage.

The central part between these two layers of compact bone is composed mainly of trabeculæ joining them. These trabeculæ are converted into a kind of meshwork by the irregular longitudinal or traction fibres mentioned above. In the upper half of the section the connecting fibres tend to run more or less at right angles to the two layers of compact bone. In the lower half or one-third their direction becomes more and more oblique, the meshwork becoming also gradually more and more open as the apex is reached. At the upper end of the bone there is also a slight tendency towards an obliquity in the opposite direction, *i.e.*, from behind upwards. The ends of the fibres near the articular surface are closer together than at their opposite ends. These fibres represent pressure lines of the patella upon the femur, and it is of interest to note that they are closest together in the upper half of the bone. The point at which they begin to fray out into the apex varies considerably, and is specially affected by the length of the bone and the development of the apex. It is also indicated that from this point downwards the patella is largely unsupported by the femur, and at the apex not at all. As it is the lower of the facets of the patella which are in contact with the femur when the knee is extended, comparatively little pressure is exerted on the femur; the patella, therefore, must be largely functionless in this position.

Special notice may be taken of the internal architecture of the apex. This apex may or may not be developed. It is especially well developed in the "large triangular" variety of the patella, which roughly forms about 12 per cent. of all patellæ. The structure may be briefly described as follows. The deeper fibres of the anterior compact layer gradually fray out into the apex. The pressure lines become markedly oblique, *i.e.*, become traction lines, and lace with the former, forming the mechanical contrivance best adapted for the support of the apex.

Sections of the patellæ of the sheep and ox were also compared with those of the human bone. They differed in being composed of far more dense bone, the more anterior and less superior insertion of the quadriceps tendon; the pressure lines directly connected the anterior and posterior layers of compact bone without the obliquity as seen in man. The structure agreed with the mechanical disposition of the bone as pointed out above. In the lower end of the bone no interlacement of the traction and pressure fibres is present like that seen in the apex of the patella of man, *i.e.*, in the quadruped the femur entirely supports the patella.

<sup>1</sup> Poirier, *Traité d'Anatomie*, 1897, p. 224, has pointed out the thinning as age advances.

PROCEEDINGS OF THE  
ANATOMICAL SOCIETY OF GREAT BRITAIN  
AND IRELAND.

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MAY 1900.

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A Meeting of the Society was held at the London Hospital Medical College, Whitechapel, E., on Friday, May 11th, at 4.30 P.M. The President, Professor YOUNG, was in the chair. Fifteen members and five visitors were present.

The minutes of last meeting were read and confirmed.

The following candidates were elected members of the Society :—  
A. Low, M.A., M.B., C.M., Senior Demonstrator of Anatomy, University of Aberdeen, proposed by W. R. Reid, A. Keith, F. G. Parsons. H. B. MYLVAGANAM, Esq., proposed by T. Openshaw, A. Keith, A. H. Young. H. BARNARD, M.B., M.S., F.R.C.S., Demonstrator of Anatomy, London Hospital Medical College, proposed by T. Openshaw, H. Rigby, T. H. Sequeira. E. ANGAS JOHNSON, M.B., proposed by A. Keith, H. Rigby, F. G. Parsons.

(1) Dr ARTHUR ROBINSON showed (a) a case of *Diaphragmatic Hernia*. The specimen was a fully developed foetus which did not breathe after birth. There was no external evidence of any abnormal condition, but when the anterior abdominal wall was removed, the only viscera discernible were the liver, the ovaries, the bladder, and a portion of the colon. On removal of the anterior wall of the thorax, the heart, pericardium, and thymus gland were found pushed over to the right side, and the left half of the thoracic cavity was seen to be occupied by the small intestine, the greater part of the large intestine, the spleen, and a portion of the stomach. The small intestine was below and in front, the vermiform appendix and cæcum

lay along the left side of the pericardium, the greater part of the colon was placed above and behind, and the fundus of the stomach and the spleen were behind the compressed left lung and the pericardium.

The left half of the diaphragm was represented by a semilunar fold of muscle attached in front and externally to the inner surface of the ribs, whilst behind and internally it terminated in a sharp tendinous margin which formed the antero-external boundary of a large orifice of communication between the abdominal and thoracic cavities. This orifice was bounded, behind and internally, by the vertebral column and the posterior wall of the thorax. Obviously, therefore, the specimen was an example of the not very uncommon condition produced by the non-union of the lateral outgrowths from the septum transversum with the dorsal mesentery of the gut.

(b) A series of lantern slides showing *the Position of the Pyloric Orifice of the Stomach* in four bodies—three females and one male—in which the viscera had been fixed by formal.

In case (A), a female 35 years old, the stomach was almost empty, and the pyloric orifice was distinctly to the right of the middle line under the centre of the quadrate lobe of the liver, on a level with the ninth right rib in the mid-axillary line, with the disc between the first and second lumbar vertebræ, and behind the right costal cartilage, midway between the mid-sternal and mid-axillary lines.

In case (B), a female 73 years old, the stomach, which was empty, had the form of a long tube slightly dilated at its upper end, to the left and behind the œsophagus, and but slightly to the right at its lower end. The pyloric orifice was to the left of the middle line, on a level with the tenth rib in the mid-axillary line.

In case (C), a female 45 years old, the stomach was moderately distended, and the pyloric orifice was to the right of the middle line, on a level with the second lumbar vertebra, and with the middle of the ninth intercostal space in the mid-axillary line, and behind the eighth right costal cartilage, midway between the mid-sternal and mid-axillary lines.

In case (D), a male 70 years old, the stomach was empty and tubular in form, with a slight dilatation behind and to the left of the œsophagus. It was bent twice on in its long axis; commencing from the fundus, it ran at first forwards and to the right, then downwards with a slight inclination to the right; and finally backwards and to the right to the pylorus, which lay on a level with the ninth right rib in the mid-axillary line, with disc between the first and second lumbar vertebræ, and behind the eighth right costal cartilage, midway between the mid-sternal and mid-axillary lines.

The conclusions drawn from the specimens were:—

1. That the condition of distension of the stomach has not much effect upon the position of the pyloric orifice.

2. That the position of the pyloric orifice is largely dependent upon the length of the small omentum.

(c) Lantern slides illustrating *the Positions of the Pulmonary, Aortic, Mitral, and Tricuspid Orifices of the Heart* in two formal hardened bodies—one a male body 70 years old, and the other a female 45 years old, affected with slight lateral spinal curvature, the convexity of the curve being to the right side.

In both cases the centres of the pulmonary and mitral orifices were in almost the same vertical plane, and the centre of the aortic orifice was slightly to the right of the centre of the pulmonary and mitral orifices.

In the male, the centre of the pulmonary orifice was behind the left margin of the sternum, on a level with the middle of the sternal end of the fourth costal cartilage.

The centre of the aortic orifice was behind the sternum, on a level with the upper part of the sternal end of the fifth left costal cartilage, and the centre of the mitral orifice was behind the left margin of the sternum, on a level with the lower part of the sternal end of the fifth left costal cartilage.

The centre of the tricuspid orifice was behind the right margin of the sternum at the lower edge of the sternal end of the fifth right costal cartilage, which was slightly lower than the corresponding margin of the fifth left cartilage.

The distance between two vertical lines drawn through the centres of the tricuspid and mitral orifices was 30 mm., and the width of the sternum at the level of the fifth intercostal space was 24 mm.

In the female, the centre of the pulmonary orifice was behind the upper margin of the third left costal cartilage, 32 mm. from the left border of the sternum. The centre of the aortic orifice was behind the lower margin of the same cartilage, 29 mm. from the margin of the sternum. The centre of the mitral orifice was just above the upper margin of the fourth left costal cartilage, and vertically below the centre of the pulmonary orifice.

The centre of the tricuspid orifice was behind the sternal extremity of the left fifth costal cartilage.

The distance between vertical lines drawn through the centres of the mitral and tricuspid orifices was 29 mm., and the width of the sternum at the level of the tricuspid orifice was 29 mm.

(d) Lantern slides and dissections illustrating *the Relation of the Tonsil to the Facial and External Carotid Arteries*.

Mr M'ADAM ECCLES said that he was particularly interested in the specimen of diaphragmatic hernia shown by Dr Arthur Robinson. He asked for the exact position of the diaphragm through which the hernial protrusion had taken place. He believed that these protrusions were nearly always found on the left side, and were attributed to a want of development of the muscular tissue of the diaphragm, possibly as the outcome of abnormal distribution or imperfect formation of the phrenic arteries. He would be glad to know whether Dr Robinson could inform him as to the occurrence of similar deformities on the right side, where actual passage of the abdominal viscera into the thorax would be unlikely, owing to the solidity of

the liver. The displacement of the heart over to the right might lead to the erroneous supposition of the presence of transposition of viscera.

With regard to the position of the pylorus, this was a matter of considerable importance to the operating surgeon, and Mr Eccles still thought that the distension or otherwise of the viscus played some part in determining the place at which the pyloric end might be situated. In cases of obstruction at the pylorus, with extreme dilatation of the organ, it was the rule to find the entrance into the duodenum well over the right side of the middle line, and it was particularly easy to perform a gastro-enterostomy well away from this region in consequence. But, on the other hand, in instances where there was a constriction of the œsophagus, the stomach was apt to be much contracted, and then he had found the pylorus to lie invariably on the left side, and it was extremely difficult to make an opening into the fundus of the organ, as museum specimens of gastrostomy only too often showed.

The relationship of arteries to the tonsil was also of great practical importance, and Dr Robinson must be congratulated on his beautiful dissections, proving the close proximity of the facial artery to the structure. On removing the tonsil by the guillotine, it was usually the habit of surgeons to press inwards at a point a little below and behind the angle of the mandible; but from these dissections, it would appear that this is somewhat a risky proceeding, as tending to bring the facial vessel in closer relationship to the tonsil and the cutting instrument.

(2) Mr PARSONS made some remarks on *the External Semilunar Cartilage of the Knee in the Primates*. He said that he had already treated the subject in his Hunterian Lectures, and that the only excuse he had for returning to it was, that he had recently obtained a good deal of fresh material. The lemurs and marmosets, he said, seemed to have the generalised mammalian condition of the cartilage as far as its posterior attachment went; that is to say, it was attached to the back of the outer side of the inner condyle of the femur. In all the monkeys and apes he had examined, exclusive of the marmosets, the external semilunar cartilage formed a complete ring, and was semilunar only in name. The knee-joint of a chimpanzee was exhibited, and Mr Parsons stated that he had found a similar arrangement in the orang as well as in a large and representative series of both platyrrhine and catarrhine monkeys. As he had never had the chance of examining a gorilla's knee, he was not quite certain where the transition to the human arrangement occurs, but the presence of the three types of meniscus in the order struck him as interesting.



(3) *Two Cases of Cervical Ribs.* By LLEWELLYN C. P. PHILLIPS, M.A., M.B., B.C., F.R.C.S., Demonstrator of Anatomy, St Bartholomew's Hospital.

The two cases detailed below occurred in subjects in the dissecting-room of St Bartholomew's Hospital during the last winter session.

The two cases together are interesting, as in the first, a male, there was a very well-developed cervical rib, practically reaching to sternum on the right side, and well developed on the left. The same body had also a deformity of one of the costal cartilages, which seems to be rare, only one author drawing special attention to it (fig. 2). The vertebræ also showed abnormalities—a spina bifida of the axis, and fibrous union of the arch with the body of the fifth lumbar vertebra.

In the second case, a female, the cervical ribs were more feebly developed, and only the right was movable. There was, however, attached to the sternum on each side a costal cartilage, a fibrous band filling up the gap. The sternum and ensiform cartilage showed foramina.

In each case the vertebra formula was normal, so these two cases are true examples of cervical ribs.

The relations of the vessels and muscles are fully given, and it will be noted in each, the arch of the aorta reached up to the level of the top of the manubrium sterni.

No. 1. *Male Subject.*—*A pair of well developed movably articulated cervical ribs. Spina bifida of axis; bifid costal cartilage, fifth lumbar vertebra in two separate portions.*

Vertebral formula, C. 7, D. 12, L. 5, S. 5.

*Condition of the vertebral column :—*

*Atlas.*—The centre of the posterior arch is deficient; the gap, measuring  $\frac{1}{8}$  in., is filled up with strong fibrous tissue.

*Axis.*—Spine bifid.

*3rd cervical.*—The spine bends to the left near its tip, appearing to represent the left half of a bifurcation.

*4th cervical.*—The spine is bifid, but the left fork is larger.

*5th, 6th, and 7th cervical.*—Spines are not bifid.

The thoracic vertebræ are normal, save that the spine of the tenth resembles that of the anticlinal vertebra.

The fifth lumbar vertebra is in two portions, the anterior consisting of the centrum and superior zygapophyses, the posterior of the arch, spine, and inferior zygapophyses, the two portions being connected by strong ligaments.

*Description of the ribs :—*

1 pair cervical ribs

12 pairs thoracic ribs = 26.

*Cervical ribs.*—

On the right side it resembles a well-formed normal first thoracic rib, possessing a head, neck, tubercle, and body, and articulates with a cartilage in front (fig. 1).

The head articulates with the body of the 7th cervical vertebra, with the intervertebral disc, and slightly with the body of the 6th cervical vertebra; its tubercle articulates with the transverse process of the 7th cervical vertebra.

On the inner border of the body is a well-marked scalene tubercle, with a groove behind it for the subclavian artery and the inferior trunk of the brachial plexus.

In front, at its articulation with its cartilage, it is broader than the cartilage and projects below it, the upper border of the rib and cartilage being in the same line.

Its costal cartilage unites at its other end with the cartilage of the first dorsal rib and is ossified.

At the upper end of the manubrium sterni is a rod of cartilage half an inch long, articulating with the manubrium and touching the cartilage of the cervical rib; at its sternal end there is a gap between it and the first dorsal costal cartilage; this rod seems to represent the sternal portion of the cervical costal cartilage.

On the left side the rib is shorter and narrower, and neither reaches the sternum nor the first dorsal rib.

It consists of a head, neck, tubercle, and body.

Its head articulates with the body of the 7th cervical vertebra, with the intervertebral disc, and slightly with the body of the 6th cervical vertebra. Its tubercle articulates with the transverse process of the 7th cervical vertebra.

Its body in front is pointed, and is connected with the upper end of the manubrium sterni by a fibrous band. There is no costal cartilage.

Its upper surface is grooved for the inferior trunk of the brachial plexus, a scalenus minimus muscle raising the subclavian artery off the rib.

*Muscles attached to the cervical ribs.*—

*Right side.* Scalenus anticus.

„ medius.

Pair of intercostal muscles.

*Left side.* Scalenus anticus.

„ minimus.

„ medius.

Pair of intercostal muscles.

The scalenus anticus on the left side is attached to the rib, close to its tip, and there is a slight indication of a tubercle; part of this muscle is separated off as a *scalenus minimus*, which is inserted into the rib between the subclavian artery and the brachial plexus, lifting the former off the bone.



*The intercostal muscles.—*

The right external intercostal of the cervico-dorsal interspace is thick and its fibres vertical, and extends from one end of the space to the other; the lower attachment is to the outer surface of the 1st dorsal rib, to a deep groove, as on a typical 2nd dorsal rib.

The internal intercostal muscle is only present at the hinder end of the space, and its fibres are horizontal.

Between the two muscles there is a stratum of fascia containing some strong fibres, which run obliquely in the direction of the typical internal intercostal muscular fibres.

The left external intercostal muscle is thick, as on the right side; and the internal intercostal muscle does not extend quite to the tip of the rib; in front it is represented by fibrous fibres.

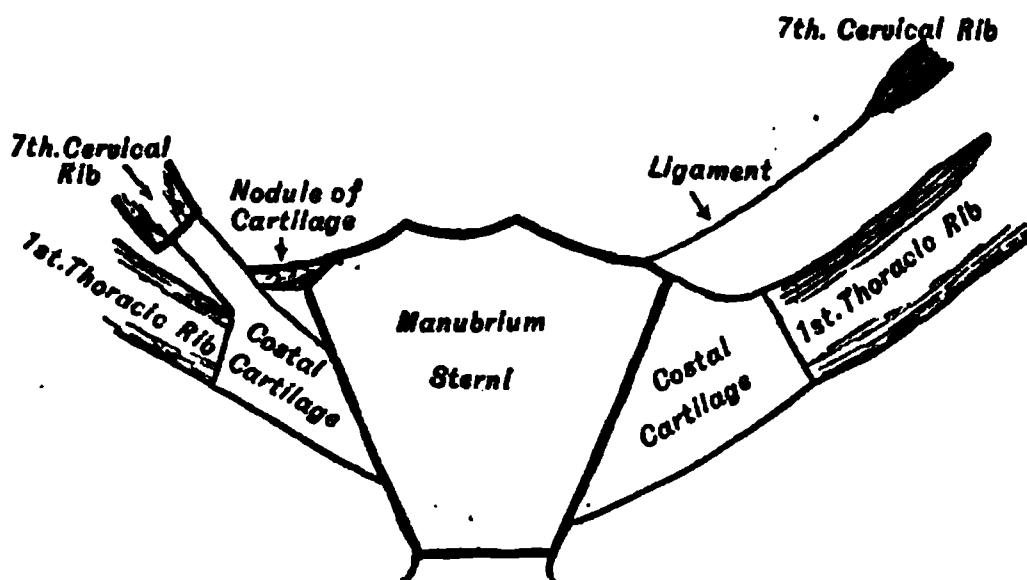


FIG. 1.—Diagram of the Cervical Ribs in Case 1.

There was no attachment of the serratus magnus on either side to the cervical ribs.

*Thoracic ribs.—*

The first thoracic rib on either side has the character of a normal second thoracic. (For measurement, see below.)

The first right costal cartilage is attached to the side of the manubrium sterni along a line  $1\frac{1}{4}$  inch long, its lower border is straight, and  $1\frac{3}{4}$  inch long at its outer end; below it articulates with the first dorsal rib, and above it is continuous with the costal cartilage of the cervical rib.

At its attachment to the dorsal rib it is  $\frac{5}{8}$  inch, to the cervical cartilage  $\frac{1}{2}$  inch, the length from the manubrium sterni to where the rod of cartilage from the sternum touches the cervical costal cartilage is  $\frac{3}{4}$  inch.

It is not ossified.

On the left side the cartilage is fan-shaped, and unites with the manubrium along a line  $1\frac{3}{4}$  inch long; between the upper border and clavicular facet is an interval of  $\frac{1}{2}$  inch.

Its lower border is 2 inches long.

Its upper border is  $\frac{1}{2}$  inch long.

The cartilage of the 3rd thoracic rib on the right side is  $2\frac{1}{2}$  inches long and  $1\frac{1}{2}$  inches from the sternum bifurcates; the upper portion of the bifurcation is free and pointed, and  $\frac{1}{2}$  inch in length, and gives origin to the internal intercostal muscle.

The 3rd thoracic rib at its sternal end is broader than the cartilage, the upper portion of it being free, whilst the lower border of both rib and cartilage are in a line.

The appearance at first suggests injury, with displacement of the upper portion of the cartilage; but Arbuthnot Lane has recorded two similar cases (*vide* Bibliography) of a costal cartilage of about the same level.

Seven thoracic ribs articulate with the sternum.

The twelfth thoracic rib is short.

No other rib calls for comment.

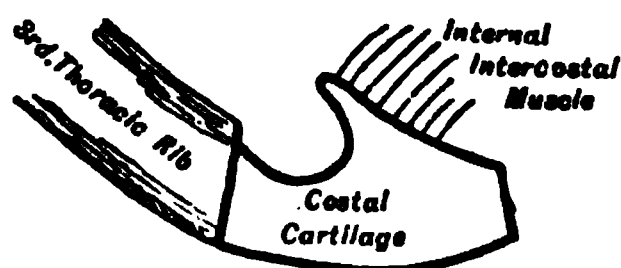


FIG. 2.—Diagram of bifurcated 3rd Costal Cartilage in Case 1.

#### *Dimensions of the Ribs.*

**7th Cervical.**—*R.* Chord head-tip,  $2\frac{5}{8}$  inch.  
Convex border head-tubercle,  $1\frac{1}{4}$  inch  
tubercle-tip,  $3\frac{1}{2}$  inches =  $4\frac{3}{4}$ .

*L.* Chord head-tip,  $2\frac{1}{2}$  inches.  
Convex border head-tubercle,  $1\frac{1}{4}$  inch  
tubercle-tip,  $3\frac{1}{8}$  inches =  $4\frac{5}{8}$ .

**1st Thoracic.**—*R.* Chord head-tip,  $3\frac{1}{2}$  inches.  
Convex border tubercle-tip, 6 inches.

*L.* Chord head-tip,  $3\frac{1}{4}$  inches.  
Greater nerve tubercle-tip,  $6\frac{1}{2}$  inches.

**12th Thoracic.**—*R.* 2 inches.  
*L.*  $1\frac{1}{2}$  inch.

#### *Sternum.*—

The manubrium sterni is 3 inches long, and the left half is rather bigger than the right; the right border sloping off from its lower end upwards and outwards, more obliquely than the left.

The 1st thoracic c.c. is joined to it on either side, and the above-mentioned cartilage rod on the right side. Its greatest breadth is  $2\frac{3}{4}$  inches, its narrowest 1 inch.

At the junction of manubrium and body, the 2nd dorsal rib on each side articulates.

The gladiolus is  $3\frac{1}{2}$  inches long.

The ensiform cartilage 2 inches.

*The upper opening of the thorax* is asymmetrical. Its antero-posterior diameter is  $2\frac{1}{2}$  inches, its transverse  $3\frac{3}{4}$ . The median antero-posterior diameter cuts the transverse  $1\frac{1}{2}$  inches from the right side.

*Arterial system.*—

The aortic arch reaches to the level of the manubrium sterni, so that the left subclavian artery has practically no intrathoracic course.

The left common carotid arises from the commencement of the innominate artery.

The right subclavian artery bends up from the innominate to pass over the cervical rib, thus taking a rather sigmoid course, the first stage lying directly behind the right common carotid.

The right vertebral artery is given off from the right subclavian  $\frac{1}{2}$  inch above its origin, and is about the diameter of the radial artery at the wrist.

It passes into its canal through the 5th cervical, as to transverse process.

The left vertebral is large, being about three times the size of the right, and also enters the 5th cervical vertebrachial foramen.

The right deep cervical artery comes off directly from right subclavian, and after running parallel with the vertebral artery, turns backwards between the 5th and 6th cervical vertebræ.

There are two deep cervical arteries on the left side: one arises from the superior intercostal, and turns back between the 6th and 7th cervical vertebræ; the other arises independently, and turns back between the 5th and 6th cervical vertebræ.

The left innominate vein is in front of the arch of the aorta, and the left vertebral vein passes *behind* the subclavian artery to join it.

The brachial plexus was nominally constituted the lowest trunk formed of the 8th cervical nerve, and the 1st dorsal crossed over *the cervical rib*, grooving it. On the left side, the continuation of the first dorsal nerve supplied both the space between the 7th cervical and 1st thoracic rib and the space between the 1st thoracic and 2nd thoracic ribs. It was not possible to ascertain the nerve supply of the supernumerary space on the right side without seriously damaging the specimen.

No. 2. *Female Subject.*—*A pair of cervical ribs, movably articulated on right side, fixed on left side.*

Vertebral formula—C. 7, D. 12, L. 5, S. 5.

*Condition of the vertebral column.*—Some osteo-arthritis present.

5th and 6th cervical vertebræ are fused, nearly completely, but their spines are almost free.

The transverse process on the left side of the 7th cervical vertebra, as viewed from behind, is more anterior than the other transverse processes.

The spines of the lumbar vertebræ show a tendency to bifurcation.

*Condition of the ribs:*—

1 pair cervical  
12 pairs thoracic = 26.

*The cervical ribs.—*

*The right one* is movable, and articulates with the body and transverse process of the 7th cervical vertebræ, and it consists of a head, neck, tubercle, and short body.

The upper surface of the body is deeply grooved for the brachial plexus and the subclavian artery, and ends in front in a rounded point at the insertion of the scalenus anticus. The whole rib is large, and triangular behind as far as the groove, and narrow in front.

From the tip a fibrous band runs to a cartilage which articulates with the sternum above the first dorsal cartilage.

*The left rib* is continuously ossified to the transverse process, as in a typical 7th vertebra, but it projects beyond the general line of costal processes, and its tip is connected by a fibrous band to a cartilage which articulates with the sternum above the first dorsal cartilage, as on the right side.

This costo-transverse process has two foramina in it, through the anterior of which runs a small branch of the superior intercostal artery, and thence inwards along the 7th cervical nerve.

The length of the rib is difficult to estimate (see below for full measurement), but from the outer margin of the main foramen to the tip the bone is 1 inch long (the normal measurement being about  $\frac{1}{16}$  to  $\frac{1}{4}$  inch).

It is grooved for the brachial plexus.

The cartilage is continuously ossified with the sternum, and is difficult to measure.

From this cartilage runs a *second* fibrous band horizontally to the inner border of the first thoracic rib; this second band is  $2\frac{1}{4}$  inches long.

The relation of the scalenus anticus to the bands is peculiar; no similar arrangement seems to have been described previously. The muscle passes *behind* the band, which stretches between the cervical rib and its costal cartilage, and is inserted into the lower band between the first thoracic rib and the cervical costal cartilage.

*Muscle attached to the Cervical Ribs.*

*Right.* Scalenus medius.

Scalenus anticus (and to ligament).

External intercostal.

(? Internal intercostal; the muscles were too damaged to be certain of).

*Left.* External intercostal.

? Internal intercostal.

The scalenus anticus was inserted at the lower band, as described above.

The serratus magnus was not attached to either cervical rib.

*Thoracic ribs.*—Seven pairs true ribs. All the ribs were slender.

The first thoracic rib on either side has the character of a normal second thoracic rib (*vide* measurements).

The right first thoracic costal cartilage was larger at its attachment to the sternum than the left.

The 7th thoracic costal cartilages unite with each other in front of the junction of the ensiform cartilage with the body of the sternum.

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FIG. 3.—Diagram of the Cervical Ribs in Case 2.

*Dimensions of the Ribs.*

- 7th Cervical.**—*R.* Chord head-tip,  $2\frac{1}{2}$  inches.  
 Convex border tubercle-tip,  $2\frac{3}{4}$  inches.  
 Ligament,  $1\frac{1}{2}$  inch.  
 Cartilage,  $1\frac{1}{8}$  inch.  
 Breadth at tubercle,  $\frac{9}{16}$  inch.  
 " groove,  $\frac{5}{16}$  inch.  
*L.* Rib from foramen to tip, 1 inch.  
 Ligament,  $3\frac{1}{2}$  inches.  
 Cartilage along upper border,  $\frac{3}{4}$  inch.  
 " along lower border,  $1\frac{1}{2}$  inch.  
 Breadth,  $\frac{5}{8}$  inch.
- 1st Thoracic.**—*R.* Along convex border tubercle tip,  $6\frac{1}{2}$  inches.  
 Cartilage,  $\frac{3}{4}$  inch along upper border.  
 "  $1\frac{7}{8}$  inch along lower border.  
 Breadth at sternum,  $1\frac{1}{2}$  inch.  
 " rib, 1 inch.  
*L.* Along convex border tubercle-tip,  $7\frac{1}{2}$  inches.  
 Cartilage lower border,  $1\frac{3}{4}$  inch.  
 Breadth,  $\frac{3}{4}$  inch.

12th Thoracic.—R.  $1\frac{1}{4}$  inch.  
L.  $1\frac{1}{2}$  inch.

*Sternum.*—

The manubrium and body are so ossified that the angle is scarcely visible.

Opposite the 5th dorsal costal cartilage is a sternal foramen,  $\frac{1}{4}$  inch in diameter.

The ensiform cartilage is partly ossified above, and also has a foramen in it, oval in shape, with its greater diameter vertical.

The vertical diameter,  $1\frac{1}{8}$  inch.

The horizontal diameter,  $\frac{9}{16}$  inch.

The 7th dorsal costal cartilages touch each other in front of the ensiform cartilage.

|                      |   |   |                        |
|----------------------|---|---|------------------------|
| Length of manubrium, | . | . | $2\frac{3}{4}$ inches. |
| „ gladiolus,         | . | . | 3 „                    |
|                      |   |   | <hr/>                  |
|                      |   |   | = $5\frac{3}{4}$ „     |

*Upper opening of the Thorax* was of a rounded shape (*vide* fig. 3), and its dimensions were as follows:—Antero-posterior (c - c)  $3\frac{1}{2}$  inches. Transversely, between the tip of the right 7th cervical rib and the middle of the ligament on the left side (A - A) 4 inches, but, as the diagram shows, these joints appeared much more as parts of the roof of the upper portion of the thorax, and a measurement between 1st thoracic rib (B - B) was taken, and was  $5\frac{3}{8}$  inches.

*Arterial System.*—

As in the first specimen, the aorta rises to the level of the upper border of the manubrium sterni, and the left subclavian artery has practically no intrathoracic course. It runs over the upper ligament.

The branches of the arch of the aorta are normal. The deep cervical artery on the right side has been damaged.

On the left side it passes backwards between the transverse processes of the 6th and 7th vertebræ.

There are many small ascending cervical branches.

The brachial plexus was normally constituted; and, as in the first case, the lower trunk formed by 8th cervical and 1st dorsal crossed over the 7th cervical rib and deeply grooved it.

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The preceding seem to be the only cases of atrophied 1st thoracic ribs recorded; and since some of them have been described without the vertebrae having been counted, it is reasonable to doubt whether all were atrophied thoracic ribs, and so they have been appended to the bibliography of the cervical ribs.

(4) *A Note on the Development of the External Malleolus.* By  
J. H. F. WILGESS.

The object of this paper is to bring before your notice a condition which seems to be common, but which is the exact opposite of the condition described in the text-books of anatomy in ordinary use.

I refer to the relative length of the tibia and fibula in foetuses earlier than the 7th month.

In Quain's *Anatomy* we find,—

"The fibula in the embryo at an early period is nearly as large as the tibia, and articulates with the femur. The tibial malleolus, on the other hand, up to the 7th month of foetal life, is longer than the fibular; and the marked preponderance of the fibular malleolus, which is peculiar to man, is only acquired after birth" (vol. ii. pt. i. p. 138, 1893).

Bland Sutton, in his article on "Osteology," in Morris' *Anatomy*, writes thus:—

"The human fibula differs from all others in the excessive length of its malleolus; in no other vertebrate does this process descend below the level of the tibial malleolus. In the majority of mammals the tibial descends to a lower level than the fibular malleolus. In the human embryo of the 4th month, the outer is very much smaller than the inner (tibial) malleolus. At the 7th month they are of equal length. At birth, the fibular malleolus is longer, and by the 2nd year it assumes its adult proportions."—*Treatise on Anatomy*, ed. by Morris, p. 159, 1898.

In the English translation of Wiedersheim's *Structure of Man*, we find,—

"Until approximately the 7th month of foetal life the tibial malleolus is larger than the fibular, projecting farther than the latter. In the 7th month the two appear to be about equal, and



then the fibular begins to take the lead. These phases are accompanied by corresponding modifications in the astragalus."

The three anatomists mentioned above cite Gegenbaur as their authority.

The present inquiry was undertaken on account of some observations made on dried preparations of 15 human foetal skeletons: 4 limbs were not entire; in the remaining 26 it was noted that the lower end of the shaft of the fibula extended below the lower end of the shaft of the tibia.

The question which presented itself was, "Whether the lower epiphysis of the tibia was really of such a size that, in spite of the preponderance of the shaft of the fibula, the internal malleolus extended below the external?"

Two methods were adopted in trying to settle the point:—

- 1. The foot was carefully disarticulated from the bones of the leg.
- 2. Sections were cut through the lower end of the tibia and fibula, the section also being carried through the foot.

The chief difficulty which presented itself was the determining whether the section had been carried through the most distal point of each malleolus. The difficulty arose from the fact that the lowest points of the two malleoli are not in the same plane.

When the section had been cut, or the foot removed, the distance that one malleolus extended below the other was measured. The following results were obtained:—

|      | Age of Fœtus. | Malleolus which extended Lower. | Distance which Malleolus extended Lower. |
|------|---------------|---------------------------------|--|
| I.   | 5th Month.    | { R. external.                  | 1.5 mm.                                  |
|      |               | { L. „                          | 1.5 mm.                                  |
| II.  | 5th „         | { R. external.                  | 1.5 mm.                                  |
|      |               | { L. „                          | 1. mm.                                   |
| III. | 4th „         | { R. external.                  | 0.5 mm.                                  |
|      |               | { L. wanting.                   |  |
| IV.  | 4th „         | { R. external.                  | 0.75 mm.                                 |
|      |               | { L. „                          | 0.5 mm.                                  |
| V.   | 3rd „         | { R. external.                  | 0.25 mm.                                 |
|      |               | { L. equal.                     |  |
| VI.  | 3rd „         | { R. equal.                     |  |
|      |               | { L. „                          |  |
| VII. | 3rd „         | { R. equal.                     |  |
|      |               | { L. „                          |  |

In No. III., the total length of the fœtus was 123 mm., the preponderance of the external malleolus was 0.5 mm.; the ratio which the preponderance bears to the total length is therefore 1.246.

In the human adult the ratio is about 1.134, the external malleolus extending below the internal about 0.5 inch, the total length being about 67 inches. This seems to show that the external malleolus

extends relatively to a lower level as age advances. Unfortunately, this point could not be verified in the other fetuses, as their heads had been removed for other purposes.

Some articulated skeletons of orang-utangs and chimpanzees were also examined. The results are, of course, liable to errors due to misarticulation. The skeletons, such as they were, showed the following points:—

*Orang-utang.*—

In 5 out of 6 specimens, the lower end of the shaft of the fibula extended below the lower end of the shaft of the tibia.

In 7 out of 7 specimens, the lower end of the epiphysis of the fibula extended below the lower end of the epiphysis of the tibia.

*Chimpanzee.*—

The shaft of the tibia in 4 specimens examined extended below the shaft of the fibula.

In 3 specimens of 8 examined, the lower end of the epiphysis of the fibula extended below the lower end of the epiphysis of the tibia. In one of these cases the shaft of the tibia extended below the shaft of the fibula.

Too much reliance must not be placed on dry specimens: the fresh fetuses, however, seem clearly to show that the external malleolus extends below the internal at a period of foetal life much earlier than is commonly supposed.

In conclusion, I wish to state that I am indebted to Dr Arthur Keith for supplying me with material and for valuable advice.

- (5) *Note on an Outgrowth of a Lymphoid Nature from the Junction of the Large and Small Intestine of a Frog (Rana temporaria).*  
By F. WOOD-JONES, London Hospital Medical College, E.C.

The lymphoid outgrowth described in the following note was noticed on opening a frog whose intestine was much distended by a

FIG. 4.—The Outgrowth *in situ*.—I, ileum; C, colon; L.F., lymphoid outgrowth; B.V., blood-vessel.

fatty meal administered for physiological purposes, and in subsequent dissections was found to be present in a fairly well marked degree in about 25 per cent. of the frogs examined.

The large intestine was distended to a considerable extent, the swelling being especially pronounced at its junction with the small intestine, and on the forwardly directed diverticulum of the gut normally present. There was observed, near the furrow that marks the union of the two divisions of the gut, a small movable and highly vascular appendage.

It appeared to the naked eye as a somewhat club-shaped outgrowth, slightly swollen, rounded at its distal end, and narrowing to a slight extent at its union with the gut.

FIG. 5.—Longitudinal section of junction of large and small intestines, showing collection of lymphoid tissues into well-marked follicles.—*i*, ileum; *c*, colon; *L.P.*, lymphoid patches.

It was supported by mesentery, and showed on its surface a rich network of blood-vessels.

The portion of the gut bearing the outgrowth was removed, hardened in alcohol, sections cut in paraffin, and subsequently stained by logwood and eosin.

Examination of the sections showed that the hypoblastic lining of the gut was not traceable in the interior of the outgrowth, but that the latter was wholly composed of a mass of lymphoid tissue, with a supporting structure of connective tissue, and that " " was supplied by a network of blood-vessels.

Traced inwards, the lymphoid tissue of the outgrowth is seen to be continuous with the lymphoid tissue of the gut; the blind and swollen end of the large intestine being especially rich in

lymphoid tissue, which here becomes aggregated into well-marked patches, somewhat after the manner of Peyer's patches; and it is with this thickened pad of lymphoid tissue which lines the blind end of the large intestine, and wraps round its junction with the

FIG. 6.—Section through Outgrowth.—I, ileum; C, colon; L.F., lymphoid follicle; B.V., blood-vessel.

small intestine, that the outgrowth is continuous,—the outgrowth appearing, in fact, to be a lymphoid patch that has pushed its way outwards from the lumen of the gut, and has come to take up an outstanding position on the wall. It was interesting in reference to the large amount of lymphoid tissue in the appendix vermiformis of man.

(6) Mr KEITH showed a specimen of the *Uterus of a Macacus rhesus*, nearly at the full term of pregnancy, and diagrams illustrating the condition of the cervix in the normal and pregnant condition, and the various forms in which the double-disc placenta of cynomorphous apes occurred. The stopper-like elevation found in the anterior wall of the cervix uteri of macaques and cercopitheques, which gave the cervical canal a zigzag appearance, had puzzled him as to its function, but on cutting open the uterus of a pregnant *Macacus rhesus*, shown in fig. 7, it was seen that the cervical elevation had assumed quite the appearance of a villus, and projected within the plug of mucus, in the cervix. Mucous strands could be seen to radiate from the surface of the villus, and there could be no doubt it was the active agent in secreting the mucus which sealed up the neck of the uterus in pregnancy. As far as he knew, this arrangement was found in only the two genera of Old World monkeys mentioned above.

The appearance of the placenta in Old World cynomorphous

monkeys indicated a zonular placenta in their ancestral stock. Between the anterior and posterior discs, the posterior always being the chief, the umbilical cord arising from it, there ran leashes of vessels on both sides, and some remnants of tissue, which he regarded as traces of the zonular placenta, of which two parts only now remained—the anterior and posterior discs. The anterior disc lay in the hollow of the neck of the contained fœtus, the posterior on its deflected face and breast.

In *Macacus* and *Cercopithecus*, the anterior placenta is only a little smaller than the posterior; in *Semnopithecus*, the anterior is less than one-third the size of the posterior; and this condition occurs

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FIG. 7.—Section of Uterus of pregnant *Macacus rhesus*.

also in *Macacus* as a variety. But in both *Macacus* and *Semnopithecus*, and more commonly still in *Cynocephalus*, cases were known in which the anterior placenta was quite absent, and only the single-disc form of Man, the Anthropoids, and the Cebidæ of the New World remained. There was no doubt that the early primate chorion was covered all over by villi; but it was still doubtful if human Man showed at one stage an equatorial zone of villi, representing a zonular placenta.

Breach presentation in Man appeared to be an atavism. It was

the normal mode of delivery in cynomorphous apes. But in the great Anthropoids, as in Man, a turning movement occurred about the fourth or fifth month of pregnancy, in which the head left the fundus and was directed to the os uteri.

Dr Arthur Robinson regarded the zonular arrangement of the chorionic villi in early human ova as artificial, that form never having been observed when the ovum was examined *in situ*.

PROCEEDINGS OF THE  
ANATOMICAL SOCIETY OF GREAT BRITAIN  
AND IRELAND.

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JUNE 1900.

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THE Summer Meeting of the Anatomical Society of Great Britain and Ireland was held in the Physiological Theatre, The Owens College, Manchester, on Thursday and Friday, June 21st and 22nd, commencing each day at 10.30 A.M. The President, Professor YOUNG, was in the chair. Thirty members and over fifty visitors attended the meetings. Letters regretting inability to attend were read from Professors HIS, WALDEYER, LEBOUcq, Sir WILLIAM TURNER, CUNNINGHAM, THOMSON, and many others.

The minutes of last meeting were read and confirmed.

The following election was made :—J. W. THOMSON WALKER, M.B., C.M. Edin., F.R.C.S. Eng., proposed by A. H. Young, Arthur Robinson, and F. G. Parsons.

The following communications were made :—

(1) Dr T. H. BRYCE read a further note of the *Deep Accessory Peroneal Nerve* of Ruge in Man.

In a paper published in the *Proceedings* of the Society in October 1896, under the title of "A Long Muscular Branch of the Musculo-Cutaneous Nerve of the Leg," I described a nerve which I identified with a nerve described by Ruge in the lower mammals, and called by him the "deep accessory peroneal nerve."

Since that date I have examined 45 subjects—90 extremities—and have met with the nerve in its complete form only once. In this instance the relations of the nerve are exactly as previously described.

It is a branch of the musculo-cutaneous, which, running in the substance of peroneus brevis, close to the fibula, appears in the lower third of the leg, on the posterior surface of that muscle, to which it gives branches. There is no peroneus quartus in this case as in the others previously described. Reaching the ankle, the nerve becomes very slender, and winds round the external malleolus beneath the tendons of the peronei muscles, to reach the outer border of the extensor brevis digitorum; there it divides into two delicate twigs. The one running parallel to the tendons of the peroneus brevis is lost in the fascia at the base of the 4th interosseous space; the other enters the outermost slip of the extensor brevis digitorum, in the substance of which it runs as far as the base of the metatarsal bone.

A microscopic examination of this filament dissected out of the muscle proved it to be a single funiculus, enclosing from 20 to 25 medullated nerve fibres.

I have now examined in all 110 extremities from 55 subjects, and have found the nerve as described above ending in the extensor brevis digitorum 3 times in 2 subjects, one case being bilateral, the other unilateral. In other 6 subjects I have traced it on one side as far as the ankle, where it ended in the peroneal sheath.

(2) Dr T. H. BRYCE gave a lantern demonstration of microphotographs, demonstrating the *maturation stages in the ovum of Echinus*. A full account will be published later.

(3) Dr ARTHUR ROBINSON exhibited numerous stereoscopic views of anatomical preparations.

(4) Dr DONALD exhibited specimens of *post-mortem contracted Heads*.

(5) Dr R. S. BERRY gave a lantern demonstration on the *Comparative Anatomy and Histology of the Cæcal Apex—the Appendix Vermiformis*. This communication will appear *in extenso* in the October number of the *Journal of Anatomy and Physiology*.

(6) Professor A. F. DIXON read a preliminary note, illustrated by lantern slides, upon *certain Surface Markings of the Calvarium, and their significance*. Among the most interesting of the markings present upon the surface of the calvarium are the grooves which are often found in the frontal region, corresponding to the branches of the supraorbital nerves. These grooves vary much in appearance, and may be simple or branched, shallow or deep. They are often converted in part of their course into tunnels. Sometimes they occur on one side of the cranium only. Most frequently the grooves occur beneath the outer branches of the nerve, but they also occur, in many cases, in connection with the inner branches. The grooves never cross the coronal suture. They sometimes extend upwards from the supraorbital notch,



or foramen, as far as the coronal suture ; but in other cases they begin inferiorly at a little foramen, where some branch of the nerve enters the bone. In the majority of cases they do not reach as far as the coronal suture. The formation of the grooves indicates a want of proportion between the growth in length of the overlying nerves and the amount of expansion of the underlying part of the cranium. The nerves might be looked upon as constricting cords, which become depressed in the developing bone as the cranium expands. Their formation is comparable to that of the grooves and tunnels sometimes found in the clavicle for the descending supraclavicular branches of the cervical plexus. The constricting portion of the nerve is often limited superiorly at the coronal suture, where the deep layers of the scalp are firmly bound down to the cranial wall, and inferiorly at a point where a branch of the nerve enters the bone. Hence the grooves caused by the nerves do not cross the coronal suture, even when they reach as far as it, and they often end below at a little foramen in the bone. The openings of these little foramina are directed upwards towards the coronal suture, just as the openings of the nutrient foramina of the long bones are directed towards the part of the bone where growth is most active and goes on longest. The presence of the grooves may be taken to indicate an excessive development of the frontal part of the cranium. In those races in whom the grooves are common and strongly marked, we would expect to find a tendency towards increased development and capacity of the frontal part of the cranium. On the other hand, in races in whom the grooves do not occur, or are rare and but feebly marked, we would expect to find a greater uniformity in the shape and size of the cranium, since in these complete harmony exists between the rate and amount of growth of the nerves and that of the underlying frontal region of the cranium. In this connection it is interesting to find that these frontal grooves are almost never found in Australian and Tasmanian crania, that they are rare among Melanesians, slightly more common in Polynesians, while in Negroes and Bushmen they are very common. Among Negroes they are present in over 50 per cent. of the skulls examined, and in many cases they are extraordinarily well marked. In ordinary dissecting-room crania they are present in slightly over 40 per cent. of all cases, and are sometimes very marked.

In the parietal region of the cranium, grooves for the middle temporal artery were found to be especially well marked in many of the most brachycephalic Burmese skulls. Some of these crania appear to have been artificially deformed, and the marked development of the grooves probably indicates a want of proportion in the length of the artery, and the amount of expansion of the parietal region of the cranium in these skulls.

In several young skulls (of about 3–5 years) distinct grooves for vessels were found in the occipital region. These are present on the surface of the cranium, between the superior and highest curved lines of the occipital bone. In all the specimens which showed these markings, the interval between the curved lines was not only relatively

but actually greater than that found in adult specimens. The condition was found in young Eskimo, Negro, Australian, and European skulls, and is probably associated with the more rapid growth of the posterior region of the cranium during the first few years after birth.

(7) Professor E. FAWCETT showed (a) two specimens in which the *Vermiform Appendix* was absent. Both were obtained from adults, and occurred in a series of 403 cases examined by himself and Dr J. V. Blachford at the City and County Asylum of Bristol. In neither case was there any sign of inflammation present, either recent or old standing. In one case there was a small thickening at the point of convergence of the longitudinal muscular gland of the large intestine; in the other, there seemed to be a slight hollow protrusion at the same point. In one case the caecum measured in height 6 cm. and in width 8 cm., in the other case it measured  $7 \times 7$  cm.

(b) *A supernumerary bone of the Carpus attached to the Trapezium* (see fig. 1).

This small bone, which was evidently a detached part of the ridge of the trapezium, with whose long axis its own long axis coincided, measured 7 mm. in length by 3 in thickness. It was attached to the palmar face of the trapezium by strong ligamentous bands. These

FIG. 1.—Supernumerary carpal bone, representing detached lower half of ridge of trapezium. The arrow points to this supernumerary bone. The ligaments mooring it in position are seen, and F is the tendon of the flexor carpi radialis. R is the ridge of the trapezium.

ligaments allowed it to be moved from side to side by the fingers. There was no synovial cavity between the bones. By its lower pole this bone was attached through two ligamentous bands to the palmar aspect of the base of the 3rd metacarpal bone; to its inner side the anterior annular ligament of the carpus was attached. It formed the lower part of the groove for the flexor carpi radialis muscle.

Another specimen exhibited to the Society showed the ridge of the trapezium with a deep notch in its anterior border. The part of the ridge below this notch corresponded exactly with the bone above described.

(c) A specimen showing *the long external lateral ligament continued, with scarcely any attachment to the head of the fibula, into the peroneus longus muscle.*

(8) Dr PETER THOMPSON showed three specimens of *abnormal Ureters*, obtained from the Practical Anatomy Rooms of the Owens College, Manchester.

In the first specimen two completely independent ureters were present on the right side. The kidney on this side was single, and the two ureters emerged from the normally situated hilum, one near the upper and one near the lower extremity of the gland. Below, they pierced the wall of the bladder somewhat to the right side of the superior surface, and opened internally by two orifices situated close together, and two inches from the commencement of the urethra. The left ureter was single, and its opening into the bladder was in the middle line, one inch from the urethral orifice, and the same distance from the openings of the right ureters.

In the second case, also, the ureter was double on the right side and single on the left; but the special feature in this specimen was the marked difference in the arrangement of the two ducts as they emerged from the hilum of the kidney. In the first specimen the two ureters at the hilum were equal in size, but in that now described the ureter emerging from the lower part of the hilum presented a well marked dilatation—the pelvis—about the size of a walnut, which, however, narrowed to form the ureter a little lower down. The ureter emerging from the upper part of the hilum of the kidney presented no such enlargement. Unfortunately the complete course of the two ducts could not be shown, but as far as was evident they remained quite separate.

A somewhat similar arrangement to that just described was found in a third specimen. The ureter from the right kidney was double near the hilum, but single below. As the two ducts emerged from the gland, one presented a marked dilatation, whilst the other was of uniform calibre. Three inches from the kidney, however, they joined together to form a single ureter.

(9) Mr H. H. BROOME (introduced by Professor YOUNG) exhibited a dissection obtained from the Practical Anatomy Department of the Owens College, showing *abnormalities of the Veins, the Arteries, and the Kidneys* (see fig. 2).

i. *Veins*.—The chief variation is the persistence of a left superior vena cava. This is formed by the union of the internal jugular and subclavian veins; and the resulting brachio-cephalic trunk runs down in front of the arch of the aorta and the left pulmonary artery, passes behind the main pulmonary vessel and crosses the back of the left auricle, to terminate by opening into the right. This vessel is not connected with the vena cava of the opposite side, the left innominate vein not being represented.

The following tributaries open into this brachio-cephalic trunk :—

- (A) Inferior thyroid vein.
- (B) A vein receiving the blood from the 1st and 2nd intercostal spaces.
- (C) A large vessel which commences in the ascending lumbar vein of the left side, and runs upwards on the left side of the bodies of the dorsal vertebræ, receiving the intercostal veins of the lower eight spaces. This vein apparently represents the vena azygos major transposed to the left side, and it receives tributaries across the middle line, which correspond to the venæ azygos minores, superior and inferior. That resembling the vena azygos minor superior is a large vessel which receives the third to the eighth intercostal veins of the right side. Above, this vein arches forwards over the root of the right lung to join the superior vena cava of the right side, in the same way as the normal vena azygos major; but below, it crosses the middle line over the body of the eighth dorsal vertebra to join the transposed vena azygos major.

The vena azygos minor inferior commences in the ascending lumbar vein of the right side, and after receiving the intercostal veins of the lower three spaces, crosses the body of the tenth dorsal vertebra to join the vena azygos major.

The veins from the upper two intercostal spaces on the right side join together to form a single trunk, which passes upwards, behind the subclavian vessels, to open into the termination of the internal jugular vein.

ii. *Arteries*.—The abnormalities of the arteries, which are confined to the thoracic region, would appear to have reference to a marked constriction which is present in the descending thoracic aorta, immediately below the attachment of the ductus arteriosus. It is to be noticed that this constriction does not correspond to that which is usually described as the aortic isthmus, for it is situated below the opening of the ductus arteriosus, and therefore in the position usually occupied by the aortic spindle. Arising from the descending thoracic aorta, about a half inch below this constriction, and opposite the head of the 6th rib, is a large arterial trunk which runs upwards and backwards over the heads of the 5th and 4th ribs, and behind the necks of the 3rd and 2nd ribs, to terminate by joining the left subclavian artery. This vessel, which becomes remarkably convoluted as it nears the subclavian, supplies the arteries to the upper three intercostal spaces, and in addition gives off a large branch which passes upwards and backwards, through a foramen in what appears to be a fusion of two ribs. Counting this double-headed rib as one, there are only eleven ribs on the left side as compared with twelve on the right; so it probably represents both the first and the second on this side.

The remaining seven intercostal spaces are supplied in the usual manner from the descending thoracic aorta.

Though the above description has special reference to the arteries of the left side, it would apply equally well to those of the right,

remembering, however, that on this side the first and second ribs are not fused, and that the branch running to the back of the neck, which corresponds to the *arteria profunda cervicis*, passes up in front of the neck of the first, and not through two fused ribs.

From a consideration of the arrangement of the arteries in this

**FIG. 2.**—A, left superior vena cava; B, ductus arteriosus; C, constriction in descending aorta; D, branch passing from aorta to subclavian; E, vena azygos major transposed; F, vena azygos minor superior; G, vena azygos minor inferior; H, *arteria profunda cervicis* passing up through I which represents the 1st and 2nd ribs; K, connecting portion of kidneys; L, inferior mesenteric artery; N, pelvis of kidney; P, branch to right kidney from right common iliac.

region, it seems probable that this large vessel, passing between the subclavian and the descending thoracic aorta, is a reinforcing branch to the latter, produced by an enlargement of the anastomosis between

the superior intercostal artery and the upper aortic intercostals. It is obvious that such a condition might easily be produced if the constriction of the aorta described above be enough to prevent a sufficient supply of arterial blood passing into the descending thoracic aorta; and the great narrowing at this constriction, together with the bilateral arrangement and convoluted course of the compensatory vessels, point to such a conclusion.

iii. *Kidneys*.—The abnormality in this region consists in the union of the two kidneys across the middle line, to form a so-called 'horse-shoe' kidney. Of the two elements, the left is three times the size of the right, and the greater part of both is situated within the false pelvis. The connecting portion, which is quite as broad as the right kidney, is placed in front of the aorta, and has the inferior mesenteric artery passing down on its anterior surface. The pelvis of the left kidney is somewhat dilated, and occupied by a large stone. That of the right is not so large, and is situated in front of the inferior vena cava, immediately to the right of the middle line.

With regard to the arterial supply, the left renal artery is three or four times as large as the right. The right kidney, however, receives a branch from the common iliac artery of that side, which runs upwards to sink into its lower margin. There is no corresponding branch present on the left side.

A special branch springs from the front of the abdominal aorta, and runs down to enter the substance of the connecting portion.

(10) Dr T. R. W. ARMOUR exhibited the *Genito-urinary Organs of a male Jerboa* (fig. 3). The chief interest of the specimen lies in the character of the glans penis, in which a condition occurs similar to that found in some reptiles, and among mammals, in certain rodents only, *e.g.*, guinea-pig, Agouti rat, and spotted cavy.

The testicle is  $\frac{3}{4}$  inch long, and nearly  $\frac{1}{2}$  inch wide; it is connected with the parietes by a mesorchium in which lie the spermatic vessels and the tortuous vas deferens, the latter having a very narrow attachment to the upper pole of the testicle, and swelling out into an ampulla before joining the urethra. The bladder is small, and has a relatively long thin neck, the upper portion of which is joined by the two ureters. The membranous urethra is nearly an inch long; at its upper end a small swelling, apparently corresponding to the prostate, can be felt: at this point the vasa deferentia and seminal vesicles join the urethra. The penis is  $1\frac{1}{2}$  inches in length; it consists of the normal corpora cavernosa and corpus spongiosum, the former diverging posteriorly as the two crura, and the latter expanding at its ends to form the bulb and glans penis. The bulb indicates on its surface a division into two hemispheres, and attached to the urethra at its posterior border are well developed Cowper's glands.

The glans penis projects backwards into the cavity of the inversion of the skin of the abdominal wall which forms the preputial sac, and

which shows the orifice of the anus upon its posterior wall. The glans is relatively large, oval in outline, and flattened on its dorsal and ventral surfaces. On the ventral aspect is a capacious meatus bounded by fissured lips. On the dorsal surface are two long horny spines lying in apposition to the surface, with their points projecting beyond the apex of the penis; these are  $\frac{1}{3}$  inch in length, sharp pointed, and slightly curved; their globular bases fit into two cup-shaped depressions in the epidermal covering of the glans, forming a ball-and-socket joint, which admits of a considerable range of movement. Occupying the dorsal surface between these are numerous much shorter spines, without uniformity of arrangement or direction. The whole glans penis is studded over with minute papillæ, which are larger on the dorsal than the ventral surface. Embedded in the substance of the glans is the

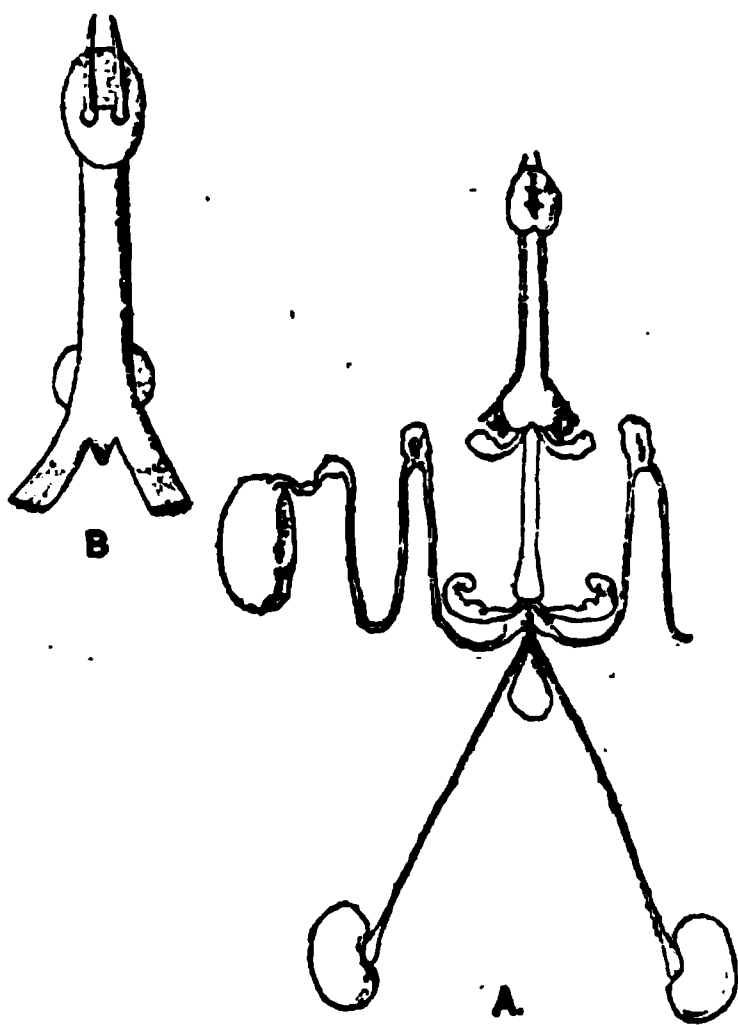


FIG. 3. —A, genito-urinary organs, Jerboa; B, penis of Jerboa (dorsal aspect).

rod-shaped os penis; the anterior end of this projects slightly into the roof of the fossa navicularis, while the posterior end lies just behind the bases of the long styles, with which it has no apparent connection.

(11) Professor A. M. PATERSON exhibited *two cases of Congenital Diaphragmatic Hernia*.

Both examples occurred by deficiency of the left half of the diaphragm in full-time female foetuses.

In one case (A) the diaphragm is almost completely absent on the left side, the only remaining portion being a sterno-vertebral band



round which the gullet bends, as it enters the abdomen. In the other case (B) the left half of the diaphragm is represented posteriorly by the sterno-vertebral band only, but anteriorly it has costal attachments (to the 7th, 8th, and 9th cartilages), and has a sharp edge which constricts the upper surface of the liver.

There is in each case a wide communication between the left pleural sac and the peritoneal cavity.

The disposition of the viscera is very similar in the two cases. The abdominal cavity contains the right half of the liver, the descending colon, and sigmoid flexure. The cæcum and vermiform appendix are displaced, lying just below in one case (A), and in the aperture leading into the thorax in the other case (B).

In the thorax in both cases the heart and pericardium are pushed over to the right side, and the left lung is small and flattened against the mediastinum, near the apex of the space. In both examples the left pleural sac is completely filled with abdominal viscera, stomach, spleen, duodenum, the loop of the colon, and the coils of the small intestines. The colon ascends between the stomach and the coils of the small intestine, and crossing the duodenum, binds it down to the posterior thoracic wall. The stomach is wholly contained in the thorax; and the oesophagus, to join it, takes a sudden bend round the left crus (sterno-vertebral band) of the diaphragm. The position of the spleen is extraordinary; by the flexion of the stomach, the cardiac end pushed upwards carries the spleen along with it. It occupies in each case a secondary hernial sac, which projects into the right pleural sac, behind the pericardium and oesophagus, and in front of the aorta.

Having recently had the opportunity of examining a considerable number of foetuses of various ages, one can state with some precision how frequent this condition is. These are the only cases of a complete hernia found in 268 foetuses between 3 and 9 months (155 male, 113 female), of which 134 are full-time (81 male, 53 female). This condition thus occurs in 0·74 per cent. of cases at all ages, and in 1·5 per cent. of cases at full time.

(12) Professor A. M. PATERSON described a case of *Left Inferior Vena Cava* (fig. 4).

The vena cava inferior begins on the left side of the bifurcation of the aorta, opposite the fourth lumbar vertebra. It passes upwards in this relation to the aorta as far as the upper border of the third lumbar vertebra, where it passes obliquely across the artery, and continues its further course on its right side. It is formed by the union of the two common iliac veins, of which the right receives the middle sacral vein. The vena cava receives also right and left lumbar veins, the left spermatic and left inferior phrenic veins, and two renal veins on each side. The right spermatic vein joins the lower right renal vein. A vein of considerable size crosses the spine behind the aorta, and connects together the right and left renal veins; it



represents presumably the remains of the original anastomosis of the embryonic vena cava, with the renal and cardinal veins. The specimen was taken from the dissecting-room, so that the arrangement of the vena azygos in relation to the vena cava inferior was not followed in detail. It was found, however, that there was nothing abnormal in the arrangement of the systemic veins in the thorax.

(13) Professor A. M. PATERSON gave a preliminary account, illustrated by numerous specimens, of the *Development and Ossification of the*

FIG. 4.—Left inferior vena cava.

*Sternum in Man and Mammals.* A full account of this communication will be found in the October number of the *Journal of Anatomy and Physiology*.

(14) Professor BIRMINGHAM exhibited (a) *Dissection of the Pelvis.* The body was hardened by intravascular injections of formalin. After opening the abdomen and removing the small intestines, the pelvis was separated from the rest of the body by an oblique cut at an angle of about 30° with the horizontal plane. The section passed just above the crest of the pubes in front, and through the 2nd sacral vertebra behind. The difficulty of dissecting the pelvis through the pelvic inlet in the ordinary way is due to the depth of the cavity and the projection of the sacral promontory. Both of these difficulties are removed by separating the pelvis in the manner described, and an excellent view of the cavity is obtained.

Having removed the peritoneum and displayed the underlying viscera, namely, the bladder, ureters, seminal vesicles, vasa deferentia, etc., the ureters were cut, and by the aid of a long curved scissors, the bladder, which was empty and contracted, was separated from the prostate and removed. In a similar manner, the vas deferens having been cut on each side, the prostate, with the seminal vesicles and the ends of the vasa deferentia attached, was carefully separated from the rectum, the pelvic floor, and the membranous urethra, and removed. The rectum, which was distended with fæces, was cut just above the beginning of the anal canal and taken out; and the visceral layer of pelvic fascia having been removed from the white line inwards, the levator ani and coccygeus were exposed. The contents of the rectum were carefully removed, with the intention of filling that organ with gelatine, but so thoroughly were its walls hardened that it retained its form perfectly, and in its interior an excellent view of Houston's valves was obtained. The various organs were then replaced in their proper positions within the cavity, and the whole pelvis built up again out of its constituent parts. The specimen affords a very satisfactory means of demonstrating the anatomy of the pelvic cavity, as each organ can be removed or restored to its place at will, without losing its shape in the slightest degree.

(b) *A case showing the Pelvic Peritoneum.*—The pelvis was separated from the body, as in the preceding specimen, the pelvic colon (sigmoid flexure) was removed, and a piece-mould of the cavity made, from which a cast was afterwards obtained. The bladder and rectum were empty and contracted, and all the folds of peritoneum well marked. The cast shows the bladder, the whole pelvic course of the vas deferens running beneath the peritoneum, the ureter, obliterated hypogastric artery, and the rectum. It also shows very clearly the plica vesicalis transversa, the paravesical, obturator, and hypogastric fossæ described by Waldeyer, and at each side of the rectum the "pararectal fossa" described by the exhibitor.

(c) *Naso-pharynx.*—A coronal section was made through the head, which passed through the nasal septum within a few mm. of, and parallel to, its posterior border. The posterior nares were particularly wide; and the whole naso-pharynx, with the openings of the Eustachian tubes, could be clearly seen through them.

(d) *Apical Gland of Nuhn.*—The anterior part of the tongue was turned up, retained in this position by a pin, and then hardened by immersion in strong formalin solution. The gland, which is over half an inch in length (almost  $\frac{3}{4}$  inch), was exposed on one side by the removal of a layer of muscle about 1 mm. in thickness, derived from the united styloglossus and inferior lingualis. On the opposite side, the four or five ducts of the glands, which open directly on the slight prominence produced by the gland, were demonstrated.

(e) *Pylorus, Plica triangularis.*—Several specimens of the pylorus, from formalin-hardened bodies, all of which were closed, and a pharynx

with the plica triangularis (His), well developed, and separated from the tonsil, were also exhibited.

(15) Professor BIRMINGHAM also read a paper on *some points in the Anatomy of the Digestive System*, which will be published in the October number of the *Journal of Anatomy and Physiology*. The paper dealt especially with the form and position of the stomach and rectum. The long axis of the stomach, traced from the summit of the fundus (not from the cardia), was described as being directed almost horizontally forwards and to the right in the male when the stomach is empty; in the female, on the contrary, as a result of tight-lacing, the long axis is often nearly vertical. Three stages were recognised in the process of distension, at the completion of which the stomach assumes an oblique position, its long axis forming an angle of about 45 degrees with both the horizontal and sagittal planes. The view was advanced that the stomach, and probably all other hollow viscera with muscular wall, were, when empty, contracted, not collapsed, their cavities following and corresponding to the amount of their contents. The large, flat-walled, and collapsed empty stomach, commonly described, probably does not exist. The pylorus, too, has never been found patent or relaxed in a body hardened by the formalin method, so far as the author was aware, and the opening of the pylorus he considers to be an active, not a passive process. Further, the pylorus is a canal of nearly an inch in length, rather than an abrupt constriction.

The rectum in all animals, when viewed from the ventral aspect, is practically straight. In man it presents a series of lateral foldings or flexures, usually three in number; and the valves of Houston are the expressions of these lateral inflections as seen from the interior of the bowel. These lateral foldings, according to the author, are an adaptation to the erect attitude, the object of which is to relieve the anal sphincters from the pressure of the rectal contents. The lateral foldings break up the rectal contents into three segments, each more or less completely supported by a valve of Houston. The view was expressed that while the levator ani and external sphincter are the true sphincters of the bowel, the internal sphincter is continuous with the circular muscular fibres of the intestine in action as well as in structure, its chief use being to empty the anal canal.

(16) Dr PETER THOMPSON gave a lantern demonstration of *the Pelvic Fasciæ and their relationship to the Levator Ani*. A full account of this demonstration will be found in the *Journal of Anatomy and Physiology*, January 1901.

(17) Dr CHARLES J. PATTEN gave a lantern demonstration on *the form of the Heart in Man and other Mammalia*. This communication will be published in the *Journal of Anatomy and Physiology* for October 1900.

(18) The PRESIDENT exhibited a series of preparations of *the posterior end of the adult Aorta*.

(19) For want of time, an important communication by the PRESIDENT and Dr ARTHUR ROBINSON on *the development and morphology of the posterior end of the Aorta and Iliac Arteries* was taken as read. It will be published at length in the next volume of *Studies from the Anatomical Department of the Owens College, Manchester*.

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